The evolution of ceratopsians

Qi Zhao

School of Earth Sciences, Faculty of Science

University of Bristol

Wills Memorial Building, Queens Road

Bristol, BS8 1RJ, United Kingdom

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Abstract

The Ceratopsia is a group of herbivorous, beaked dinosaurs from the Late Cretaceous. In my PhD thesis, I carried out research on the evolution of ceratopsians through bone histology and numerical analysis. Based on numerous specimens of *Psittacosaurus lujiatunensis* in different ontogenetic stages, a bone histological study of ontogenetic growth in *Psittacosaurus lujiatunensis* shows some differences from *Psittacosaurus mongoliensis.* Bone thin sections from individuals of particular ontogenetic ages revealed some novel aspects of dinosaur behaviour, such as posture shift and juvenile-only clusters. Numerical analyses on phylogeny, diversity and disparity show the macroevolutionary patterns of ceratopsians.

The mechanism of postural shift in *Psittacosaurus* is revealed by histological study, and the transition from quadrupedality to bipedality appears to have occurred at about age 2. Juvenile-only clusters in *Psittacosaurus*, ranging from five to 34 individuals, and with evidence for a variety of ages in at least one specimen (IVPP V14341) suggests some unique juvenile-only behaviour. The series of thin sections from *P. lujiatunensis* indicated five types of bone tissue and four histological ontogenetic stages, i.e., hatchling, juvenile, sub-adult, and adult. None of the specimens was fully-grown. *P. mongoliensis* and *P. lujiatunensis* are similar in external morphology, but their growth patterns in terms of bone histology show several differences.

According to the cladistic analysis, which combines basal and derived ceratopsians for the first time, *Chaoyangsaurus youngi* is the most basal ceratopsian, and *Yinlong downsi* is the most basal neoceratopsian, instead of *Chaoyangsaurus*

youngi. The diversity research supports the idea that the major large-bodied herbivorous ceratopsians endured about 5 Ma of decline in taxonomic diversity before their extinction. In the disparity research, basal neoceratopsians occupied the largest morphospace compared to later groups, suggesting considerable anatomical specialization through the Late Cretaceous.

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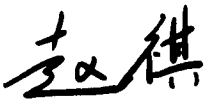
For any errors or inadequacies that may remain in this work, of course, the responsibility is entirely my own.



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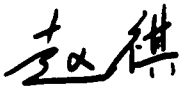
Author's Declaration

I declare that the work in this dissertation was carried out in accordance with Regulations of the University of Bristol. The work is original, except where indicated by special reference in the text, and no part of the dissertation has been submitted for any other academic award. Any views expressed in the dissertation are those of the author.

SIGNED: 

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Chapter 1 Introduction

Author Contributions: This chapter has not previously been published. All material herein is the work of Q. Zhao

During the middle Cretaceous, some 130-100 million years ago, terrestrial ecosystems were revolutionized. The trigger was the radiation of flowering plants, the angiosperms, which started from minimal diversity, but by the end of the Cretaceous, 65 million years ago, represented 70-80% of all land plants. Following the revolution in floras, social insects (ants, termites, bees) and leaf-eating insects radiated explosively, followed not long after by insect-eating and plant-eating vertebrates, notably frogs, lizards, birds, and mammals, but it seems that dinosaurs were not involved. This episode has been termed the Cretaceous Terrestrial Revolution (KTR) by Lloyd et al. (2008).

Dinosaurs radiated through the Cretaceous, and many new groups of herbivores and carnivores appeared, but not as fast as other groups that responded to the KTR. The Ceratopsia originated at about the same time as the angiosperms, and became main group of herbivores in the Late Cretaceous. Particularly significant among the earliest ceratopsians is *Psittacosaurus*, represented by ten species from Mongolia, China and Russia; the majority of these species come from the Early Cretaceous of China. This dinosaurian genus was enormously widespread, hugely abundant in its faunas, and as diverse in terms of species as many modern mammals.

Ceratopsian dinosaurs are herbivorous animals and so they suffered restrictions to their diet as the angiosperms displaced the other plant groups. With the great radiation of angiosperms, ceratopsians did not become extinct: indeed the group radiated throughout the Late Cretaceous. It would be hard to assess their migrations through time, but I can assess size and heterochronic changes. Collections in China document the early evolution of ceratopsians through the critical mid Cretaceous interval (Aptian-Cenomanian), when angiosperms were becoming established, and there are now remarkable collections of ontogenetic cycles of the basal forms

Psittacosaurus and *Protoceratops*, through hatchlings, juveniles, young adults, and mature adults (Erickson and Tumanova, 2000; Erickson et al., 2009, Dodson 1976). Numerical studies on growth and ontogenetic morphometrics are already available (Dodson 1976), but critical studies on bone histology have yet to be investigated. Research on bone histology will establish the growth patterns of ceratopsians and these can be compared with other groups of dinosaurs.

In my thesis, I will focus on bone histology, phylogeny and diversity research on ceratopsian dinosaurs, and expose the growth patterns of horned dinosaurs in the Cretaceous Terrestrial Revolution.

1.1 Bone histology work in ontogenetic research of dinosaurs

Bone histology has become a common method to ascertain the ontogenetic stage of a specimen in the description of a new dinosaur taxon (Erickson et al., 2006; Sander et al., 2006; Xu et al., 2007; Xu et al., 2012). The key observation is that avascular lamellar-zonal bone in the outermost cortex, the so-called external fundamental system (EFS) or outer circumferential lamella (OCL) (Chinsamy-Turan, 2005), indicates the ending of growth, and so allows some calibration of a life table of size vs. growth stage.

Studies on ontogenetic stages using bone histology are not very easy to perform because they require reasonable sample sizes, but they still have been done before in several different dinosaur groups, such as *Troodon formosus* (Varricchio, 1993), *Massospondylus carinatus* (Chinsamy et al., 1994), *Apatosaurus* (Curry, 1999; Klein and Sander, 2008), *Psittacosaurus mongoliensis* (Erickson and Tumanova, 2000); *Tyrannosaurus rex* (Erickson, 2005; Horner and Padian, 2004); *Dryosaurus*

lettowvorbecki (Chinsamy, 1995), *Diplodocus* (Klein and Sander, 2008), C*amarasaurus* (Klein and Sander, 2008), *Brachiosaurus* (Klein and Sander, 2008), *Europasaurus* (Klein and Sander, 2008), *Phuwiangosaurus* (Klein and Sander, 2008), *Ampelosaurus atacis* (Klein and Sander, 2008; Klein et al., 2012), and *Plateosaurus engelhardti* (Klein and Sander, 2007).

In this study, I was able to carry out a bone histological study of ontogenetic growth in the basal ceratopsian dinosaur *Psittacosaurus lujiatunensis* from the Early Cretaceous Yixian Formation of the Lujiatun locality in Liaoning Province, NE China.

1.2 Bone histology research in dinosaurs

Several studies on dinosaurs (Erickson and Tumanova, 2000; Horner et al., 2000; Klein and Sander, 2008; Klein et al., 2009) have demonstrated that histological sections of fossil bone samples can be used to establish the relative age/ontogenetic stage of specimens. Because bones are usually affected by remodelling processes a single bone does not reveal the complete growth of an individual, and overlapping histological records of younger and older individuals must be combined to elucidate the full ontogenetic growth trajectory for the species. There are many *Psittacosaurus* skeletons including juveniles to adults in the Institute of Vertebrate Paleontology and Paleoanthopology (IVPP, Beijing, China), showing every ontogenetic stage. These will allow me to explore character changes in the ontogenetic process, and establish the life history curve for *P. lujiatunensis*.

Many researchers have suggested that the age of reptiles can be determined by skeletochronology - assuming that one LAG (line of arrested growth) represents one

year of growth, with a slow-down indicated in winter (Castanet et al., 1993; Francillon-Vieillot et al., 1990; Ricqlès et al., 1991; Sander and Klein, 2005). Using this approach, Erickson and his colleagues sought to reconstruct life tables and assumed logistic growth curves for a variety of dinosaurs, such as *Tyrannosaurus*, *Oviraptor* and *Psittacosaurus* (Erickson, 2005; Erickson et al., 2006; Erickson et al., 2004; Erickson et al., 2009; Erickson et al., 2007; Erickson et al., 2001; Erickson and Tumanova, 2000). The methods have attracted a great deal of attention, even though they have been criticised by Sander et al. (2004) because sauropods evolved very large body size much faster.

Work on the ontogenetic process is well established (Erickson and Tumanova, 2000), but should be extended by more detailed sampling and by inspection of additional species. The method relies on well preserved bones, and cross sections showing lines of arrested growth (LAGs) that correspond to annual or seasonal cycles.

The technique is most reliable when juveniles and adults are sampled from the same localities where climate cycles can be assumed to have been similar for animals of all sizes. By determining numbers of LAGs, age at death can be determined, and the body size also estimated from well-established scaling formulae from the lengths and cross-sectional areas of limb bones (femur, tibia, humerus) (Horner et al., 2000). In order to minimize damage to the sampled bone, a coring method has been developed by Sander (2000). A core of approximately 10–15 mm diameter is drilled with a diamond-studded coring bit into the cortex of the narrowest mid-shaft area. To ensure the capture of the longest possible growth record the cores in long bones were always drilled through the cortex into the medullary region (Klein & Sander 2007).

Bone histology is also applied in functional morphology research (Buffrenil and Mazin, 1990; Riggs et al., 1993). The first dinosaurs were bipeds and they

switched posture to quadrupedality in their later evolution, at least four times, among sauropodomorphs, thyreophorans, derived ornithopods, and ceratopsians (Carrano, 2005; Maidment and Barrett, in press). It might then be expected that juveniles of these clades would show a corresponding switch from primitive bipedality to derived quadrupedality during growth, but that is not the case. In fact, large dinosaurs such as sauropods had quadrupedal embryos and hatchlings (Carrano, 2000; Chiappe et al., 1998; Yates et al., 2010), and some evidence (Reisz et al., 2005) suggests that bipedal adult dinosaurs may have had quadrupedal offspring. Perhaps then dinosaurian ontogeny recapitulates a much earlier condition, that of the first quadrupedal archosaurs in the Early Triassic (Hutchinson and Gatesy, 2006; Sereno, 1991), before the origin of the larger clades that include Dinosauria, the Dinosauromorpha and Avemetatarsalia, which were already bipedal. Among dinosaurs, the mechanism of postural change from hatchling to adult has remained speculative. In my research, I will show how the postural swift in *Psittacosaurus* in its ontogenetic stages though bone histology research.

In this study, I will describe the histological ontogenetic changes in *Psittacosarusu lujiatuensis,* and compared with *Psittacosaurus mongoliensis.* The growth pattern in bone histology is different between these two species, showing the complexity of growth pattern in dinosaur.

1.3 Locomotion of *Psittacosaurus*

The first dinosaurs were bipeds, but quadrupedality evolved secondarily at least in four groups: giant sauropodomorphs, thyreophorans, derived ornithopods, and ceratopsians (Carrano, 2005). However, ontogenetic studies have shown that even

some dinosaurs that remained bipedal as adults had quadrupedal offspring (Reisz et al., 2010), while conversely some dinosaurs that were quadrupedal when mature had bipedal offspring (Dilkes, 2001; Norman, 1980). The primary evidence for these postural shifts has come from allometric studies showing either shortening or lengthening of the forelimbs, relative to the hindlimbs, over the course of ontogeny. However, no study to date has simultaneously investigated both limb bone allometry and limb bone histology in any dinosaur, even though histological evidence would make it possible to establish the approximate ontogenetic ages of the specimens included in the analysis and therefore address the timing of changes in posture. Furthermore, patterns of differential growth should be reflected in the microstructure of the forelimb and hindlimb bones. Histology has considerable potential as a supplement to allometric studies of dinosaurs, particularly given that histology can provide a continuous record of the growth of an individual bone up to the time of an animal's death. By contrast, measurements of the dimensions of a limb bone offer only a "snapshot" of the size the bone had reached at that time. However, an obstacle limiting the application of histological approaches in such research is the difficulty of obtaining a sufficiently large sample of individuals whose limb bones can be sectioned for histological examination.

Psittacosaurus is among the most diverse and abundant dinosaurs, known from ten or more species and more than 1000 specimens from the upper Lower Cretaceous (130-100 Myr) of China, Mongolia, Russia, and Thailand (Sereno, 2010). It is a basal member of Ceratopsia, a group that subsequently diversified in the northern continents during the Late Cretaceous to produce a species-rich assemblage of large, horned herbivores. *Psittacosaurus* is widely interpreted as an obligate or at least habitual biped as an adult (Chinnery, 2004; Chinnery and Horner, 2007; Osborn,

1924; Senter, 2007; Sereno, 1990, 1997b; You and Dodson, 2004), and lay phylogenetically near or even within the transition to the obligate quadrupedality that was characteristic of ceratopsids and possibly some of their closest relatives (Hutchinson and Gatesy, 2006; Senter, 2007; Xu et al., 2006). For these reasons, *Psittacosaurus* is of intense interest from the perspective of dinosaurian postural evolution, and the abundance of this taxon in the Lower Cretaceous of Asia makes it a natural subject for palaeobiological analyses in which sample size is a factor. In this paper I analyse the limb proportions and histology of *Psittacosaurus* based on a sample of specimens varying in age from hatchling to adult, in order to determine whether a postural shift took place during the growth of this dinosaur and investigate the ontogenetic timing of any shift that can be inferred.

All of the 16 individuals included in the study were collected from the Lujiatun Beds (age 123.2 ± 1.0 Myr) of the Lower Cretaceous Yixian Formation exposed near Lujiatun Village, Beipiao City, Liaoning Province, China. The majority (10 skeletons) are juveniles of various ages that were preserved in clusters of individuals apparently representing the same stage of growth. One of these clusters, accessioned as IVPP (Institute of Vertebrate Paleontology & Paleoanthropology, Beijing) V14341, has previously been interpreted (Zhao et al., 2007) as resulting from burial in a volcanic debris flow that killed the animals instantly. Juvenile individuals were selected for analysis from IVPP V14341 (Fig. 1.1) and three similar clusters, but only some of the specimens in each cluster were sufficiently complete and well preserved for inclusion in the study.

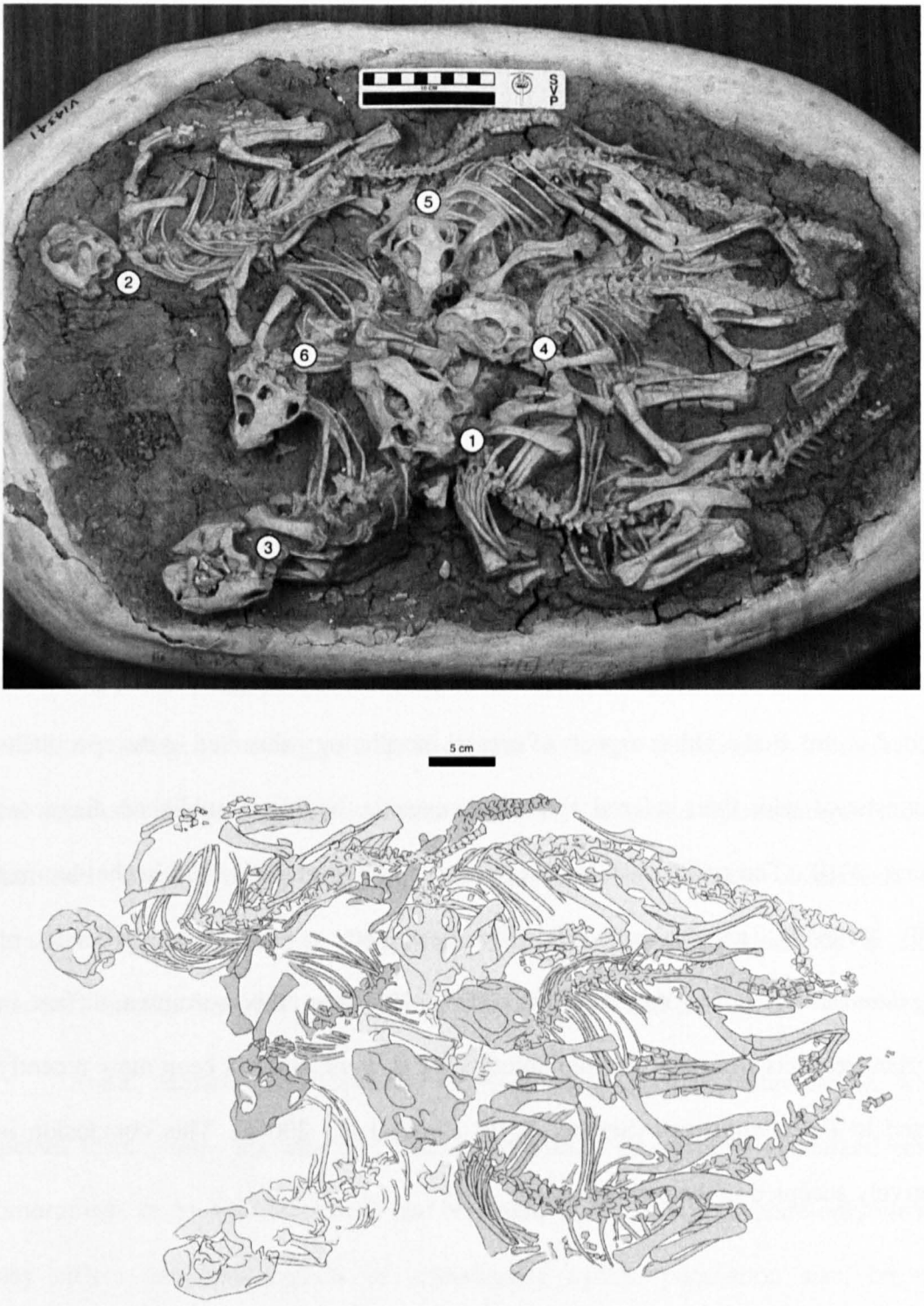

Figure 1.1 Cluster of six juvenile *Psittacosaurus* from the Early Cretaceous of Lujiatun, Liaoning Province, China

The cluster, shown in a photograph (**a**) and interpretive drawing (**b**), contains six aligned juvenile specimens. Bone histology indicates that specimens 2-6 were two years old at time of death, whereas specimen 1 was three years old.

Almost all of the individuals included in this study, including the two from the cluster described by Zhao et al.(2007), are clearly referable to *Psittacosaurus lujiatunensis* Zhou et al. Zhou et al. (2006b). All of them have narrow prefrontals, considered to be autapomorphic for *P. lujiatunensis* (Sereno, 2010; Zhou et al., 2006b). A shallow depression on the jugal is also present in all the individuals in the sample. This feature is uniquely shared by *P. lujiatunensis* and *P. major*, the only other *Psittacosaurus* species known from the Lujiatun Beds. However, *P. major* has a characteristically narrow skull roof, a trait not evident in any of the specimens included in this study. Other aspects of cranial morphology observed in the specimens are consistent with their referral to *P. lujiatunensis*, based on published diagnoses (Sereno, 2010). The only possible exception is the largest individual in the data set (IVPP V12617), which was originally described as an adult specimen of *Hongshanosaurus houi* (You and Xu, 2005). However, this specimen differs in important respects from the juvenile holotype of *H. houi*, and has been more recently referred to *P. lujiatunensis* (Sereno, 2010; Zhou et al., 2006a). This conclusion is tentatively accepted in the present study.

1.4 *Social behaviour in Pisttacosaurus*

It is hard to prove that an association of juvenile dinosaurs represents original behaviour rather than sedimentary accumulation, and it is hard also to determine the ages of such juveniles. A previously described specimen, which consists of an 'adult'

Psittacosaurus with 23 fully articulated juveniles, turns out to be a composite: the 'adult' skull has been added, and in any case it is below breeding age. Other juvenile-only clusters have been reported, but the best examples that likely reflect behaviour rather than sedimentary accumulation come from entombment beneath pyroclastic flow deposits at Lujiatun beds in NE China, Early Cretaceous. A remarkable juvenile-only cluster of *Psittacosaurus* shows clear evidence of different ages (five 2-year olds and one 3-year old) based on bone histological analysis. These juveniles may have associated together as a close-knit, mixed-age herd either for protection, to enhance their foraging, or as putative helpers at the parental nest.

Gregarious behaviour is beneficial to animals because it provides protection in numbers and gives each individual a better opportunity for survival (Alexander, 1974). Advantages of living in a flock or herd include a decreased risk of predation and increased foraging efficiency, and these may outweigh disadvantages such as increased competition for resources and increased transmission of diseases and parasites (Alexander, 1974). Gregarious behaviour has been identified in many modern animal groups, such as birds, crocodiles, fishes, and arthropods.

Some animals show specialized kinds of gregarious behaviour in which species form groups according to gender, especially where there is marked sexual dimorphism, or by age (Ruckstuhl and Neuhaus, 2000, 2001). Juvenile-only clusters may reflect particular aspects of reproductive cycles, population size, resource distribution, or environmental conditions that favour segregation of adults from their young (Main and Coblentz, 1996). Care of the young can be costly for many modern species, especially of birds and mammals, and so those species that do not care for their young after hatching gain by conserving energy that would otherwise have been required to defend and provision their offspring (Isles, 2009). Juveniles that are

abandoned after hatching or birth, as is commonly the case in groups other than birds and mammals, then gain the advantages already noted by aggregating in clusters. At small size, the main threat to life is predation, and juvenile clusters, while running the risk of attracting attention by their very existence, can aid individuals in escaping predation by scattering randomly when threatened. In some cases, the juvenile cluster might assist the individuals to master a food supply that would otherwise be out of reach.

Juvenile aggregation is uncommon in extant archosaurs such as crocodilians and birds (Isles, 2009). In modern birds like ostriches and ravens, while adults are preoccupied with breeding, nesting, and the care of eggs and hatchlings, nonbreeding juveniles and adults may congregate elsewhere in social groups of mixed age (Varricchio et al., 2008). Further, in species of birds and mammals where there are complex breeding rituals, and especially where single dominant males may build harems, the unmated juveniles or subadult males live safely in non-breeding herds, separate from the mated adults.

Numerous examples of gregarious behaviour of juvenile dinosaurs also have been noted (Forster, 1990b; Kobayashi and Lu, 2003; Varricchio and Horner, 1993; Varricchio et al., 2008). For example, Horner and Makela (Horner and Makela, 1979) first described 11 young hadrosaurs jumbled together in a nest-like structure from the Two Medicine Formation (Upper Cretaceous) near Choteau, Teton County, Montana. However, the identification of this hadrosaur 'nest' has been questioned and considered to be a secondary sedimentary mound (Isles, 2009)

Juvenile dinosaurs were unusual among terrestrial vertebrates for aggregating into what appear to have been exclusive herds or groups for an extended period of time, and with no sign of adult supervision. Juvenile clusters been reported for all

major dinosaur groups, except Pachycephalosauria, namely Sauropodomorpha (Myers and Fiorillo, 2009), Theropoda (*Megapnosaurus rhodesiensis* (Raath, 1990); *Albertosaurus* sarcophagus (Currie, 1998) and *Sinornithomimus dongi* (Kobayashi and Lu; Varricchio et al., 2008)), Ornithopoda (Iguanodon (Norman, 1987) and Tenontosaurus (Forster, 1990c)), Thyreophora (stegosaur *Stegosaurus* (Galton, 1982); ankylosaurs *Gastonia bergei* (McWhinney et al., 2004) and *Pinacosaurus* (Currie, 1989)), Ceratopsia (*Protoceratops* (Weishampel et al., 2000) and *Triceratops*(Mathews et al., 2009)). The skeletons in these bone-beds seem to have been transported to their final position by floodwaters, and so it cannot be demonstrated that the associations of numerous juvenile skeletons could not have been produced in some cases at least by sedimentary sorting and winnowing of similar-sized carcasses.

One exceptional juvenile dinosaurian assemblage is that of the ornithomimosaur theropod *Sinornithomimus dongi* (Kobayashi and Lu, 2003; Varricchio et al., 2008), preserved on the floor of a small dried-up lake. The uniform preservation, close proximity on a single bedding plane, and sub-parallel alignment of skeletons supports a catastrophic mass mortality of a group rather than the attritional death of individuals (Varricchio et al., 2008). It cannot be entirely excluded that the individuals came together at the drying lake from different sources, in search of water as the landscape dried up, and so perhaps did not live together. This bonebed site emphasizes the important role of drought in the fossil record both as an agent of mortality and as a mechanism driving vertebrates into depositional settings where preservation can occur (Rogers, 1990; Shipman, 1975)

Here, I used bone histology method to prove the first convincing example of a mixed-age juvenile group from the fossil record, an assemblage of six juvenile

skeletons of the ceratopsian dinosaur *Psittacosaurus lujiatunensis* from the Early Cretaceous of NE China which was published by (Zhao et al., 2007). I explore in Chapter 3 possible reasons for such a mixed-age cluster without adults, whether it indicates a group seeking to find food or avoid predation, or, perhaps a hint of helpers at the (dinosaur) nest. First, I consider previously reported examples of juvenile-only clusters of dinosaurs, and find that the evidence of biological, rather than geological, association is often weak.

1.5 Phylogeny of Ceratopsians

Monophyly of Ceratopsia, Psittacosauridae, Neoceratopsia and Ceratopsidae is well established (Dodson and Currie, 1990; Sereno, 1986, 1997a, 1999; Sereno, 2000; Xu et al., 2002; You and Dodson, 2003). Previous phylogenetic works on ceratopsians were just based on basal ceratopsians or derived ceratopsians, and so there was no comprehensive phylogeny of the whole clade. Here I build a super-matrix including all the ceratopsians. My analysis includes 318 characters scored for 62 in-group taxa and 1 out-group taxon, making it the largest and most complete analysis of ceratopsian phylogeny yet undertaken.

1.6 Diversity work on Ceratopsians

The diversity patterns among herbivorous dinosaurs (including ceratopsians) and plants during the Cretaceous are very interesting topics. Many hypotheses concern proposed interactions between herbivorous dinosaurs and early angiosperms during the Cretaceous period (Bakker, 1978; Bakker, 1986; Butler et al., 2009a;

Tiffney, 2004). Bakker (1978, 1986) proposed a link with the origin and early diversification of angiosperms. He considered that the shift from a high-browsing fauna (sauropods and stegosaurs) to a low-browsing fauna (ornithopods and ankylosaurs) created highly disturbed environments that favoured the evolution of the weedy, r-selected (i.e. high fecundity and short generation times) early angiosperms (Bakker, 1978; Bakker, 1986; Tiffney, 2004). Other authors subsequently proposed that the middle to Late Cretaceous radiation of angiosperms might have driven the evolution and radiation of several herbivorous clades such as ornithopods, ceratopsians and titanosaurian sauropods (Barrett and Wills, 2001; Coria and Salgado, 2005; Tiffney, 2004; Weishampel and Norman, 1989). However, Lloyd et al. (2008) found few significant diversification shifts among dinosaurs in the Cretaceous, and one of only two was Neoceratopsia. Further, Butler et al. (2009a) argued that there are no clear changes in dinosaur diversity patterns during Hauterivian-Barremian (Early Cretaceous) that could be linked to the origin or early diversification of angiosperms. Furthermore, they considered that there is no significant spatiotemporal association between particular dinosaur groups and cycads (Butler et al., 2009b).

1.7 Disparity work in dinosaurs

The assembly of a detailed data matrix offers a prime opportunity to investigate in detail ceratopsian disparity. Disparity is the range of morphology documented in a group of organisms, and it may be assessed from continuous characters, such as linear measurements (as in traditional morphometrics), or landmarks (as in geometric morphometrics). In all instances, the techniques aim to describe aspects of shape. Another source of descriptors, however, is embodied in the

character-state scores assigned to taxa. Disparity built from discrete characters has become increasingly popular, and is applied here for the first time to ceratopsians and their immediate outgroups. There have been some disparity studies on ceratopsian skull shapes, based on landmarks (Chinnery, 2004; Dodson, 1993), and the only discrete-character study by Brusatte et al. (2012) is part of a wider study of dinosaurian morphological change through the Campanian and Maastrichtian.

Here, I explore discrete-character disparity, using the cladistic data matrix (Chapter 5) as the data source. These kinds of cladistic disparity studies have been carried out before on a variety of taxa, including arthropods (Wills et al., 1994), basal dinosaurs (Brusatte et al., 2008a, b; Ruta et al., 2006), procolophonids (Cisneros and Ruta, 2010), ichthyosaurs (Thorne et al., 2011), and pterosaurs (Butler et al., 2012; Prentice et al., 2011). In all cases, there is clear evidence for decoupling (= separation) between diversity and disparity. Frequently, as was found also with continuous-character studies on disparity of marine invertebrates (Erwin, 2007), disparity generally expands first, diversity second in a diversification. This suggests that a common evolutionary pattern is for organisms to explore the limits of possible shapes and forms, and then for new species to emerge that exploit the variance in morphology, but do not further expand the scope of that morphological diversity. In other words, the limits of morphospace are often exploited early, and later subclades tend to specialize into parts of the overall morphospace.

Because of limited time, I have not been able to analyse the evolutionary rates in these groups, and this work will be continued in the future.

Chapter 2 Methods

2.1 Histological sectioning

Histological thin sections of long bones were made using standard techniques. Previous studies of dinosaur long-bone histology, as well as general principles of bone growth, indicate that a section taken at the middle of the shaft of a long bone is optimal for obtaining a maximally complete growth record from that bone (Erickson and Tumanova, 2000; Horner et al., 2000; Sander, 2000). This arises from the predominantly appositional growth of this part of the shaft, and the location of the neutral zone in this region (Sander, 2000). Specimens were embedded in resin, and mid-shaft, diaphyseal transverse thin-sections were cut using a diamond circular saw fitted with a diamond-tipped wafering blade. One surface of each section was smoothed with a wheel grinder/polisher, and then ground manually using grinding powder (600 grit) to produce a smooth texture ideal for gluing to a glass slide. The section was then cut to a thickness of about 250 μm with a diamond circular saw before being ground further to the desired final thickness of 50–80 μm, leaving the exposed surface of the section smooth. Each slide was then cleaned in a water-filled ultrasonic cleaner to remove microscopic grit, and finally capped with a glass cover slip. The completed thin sections were studied in normal and polarized light.

2.2 Age determination

The histological sections made it possible to estimate the age in years of each individual at the time of death, based on the typical pattern of formation of lines of arrested growth (LAGs) on an annual basis in dinosaur long bones. In sections that showed a small medullary cavity, the number of visible LAGs was taken to correspond approximately to the individual's age in years, although it is unlikely that each LAG was formed exactly on the anniversary of hatching. Strictly speaking, the

number of LAGs can be taken as a maximum bound on age in years, with a possible error of several months, but in this paper I use the phrase "N-year-old individual" to mean "individual in which N LAGs had formed". However, the phenomenon of enlargement of the medullary cavity during growth introduced a well-understood complication (Chinsamy-Turan, 2005), in that such enlargement occurs through internal resorption of the bone cortex that may eliminate LAGs beginning with the innermost. To avoid underestimating ages as a result of this type of erosion, I used smaller examples of the bone in question as a reference point. The section being evaluated was graphically superimposed on equivalently orientated sections from smaller bones, and any LAG from the smaller bone that was entirely overlapped by the medullary cavity of the larger bone was assumed to be missing in the latter. For example, only two LAGs are visible in the tibia of IVPP V14341.1, but superimposing the section of this tibia on tibial sections from smaller individuals indicated that the medullary cavity of IVPP V14341.1 was large enough to have subsumed the first LAG formed during growth of the tibia (Figs 2.1, 2.2). Accordingly, the LAGs visible in this specimen were identified as the second and third, rather than the first and second, and the specimen was identified as a three-year-old.

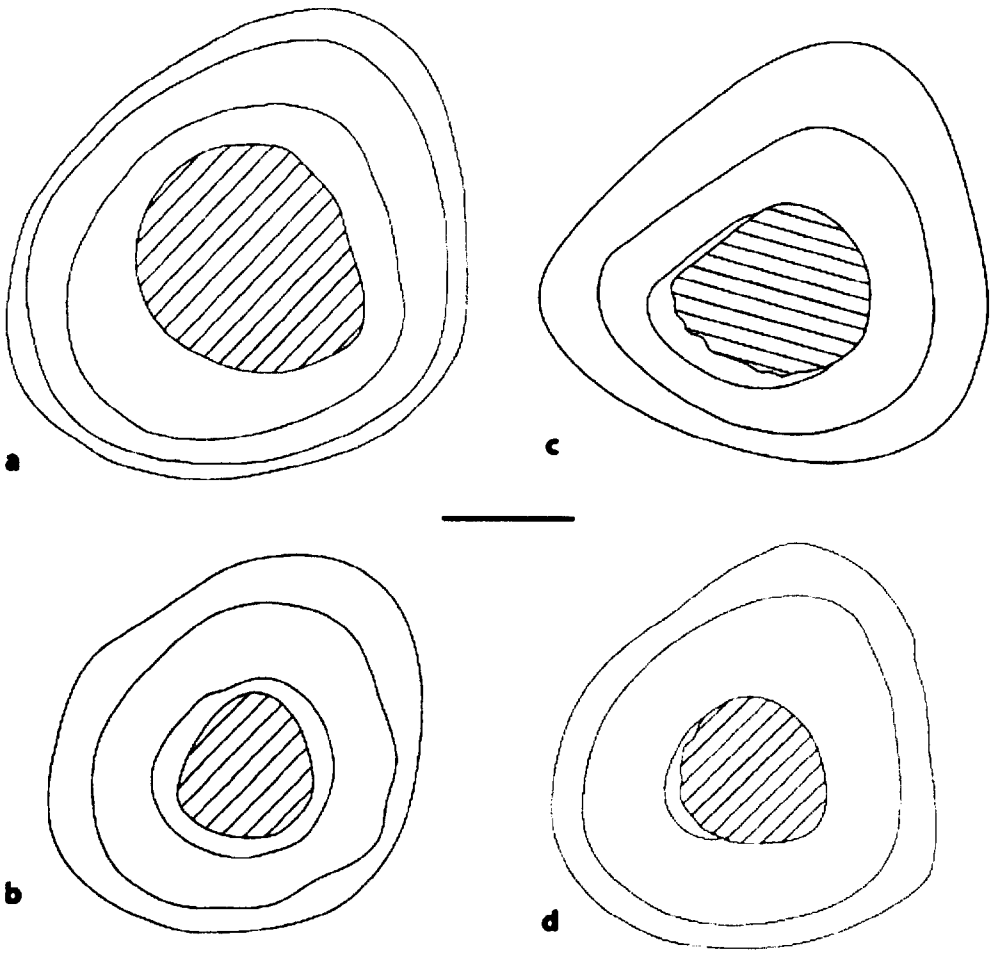

Figure 2.1 The outline and LAGs drawing in the tibiae of IVPP V14341.

IVPP V14341.1 (Fig. 2.1a), IVPP V14341.2 (Fig. 2.1b), IVPP V14341.3 (Fig. 2.1c), IVPP V14341.4 (Fig. 2.1c). Scale bar is 2 cm

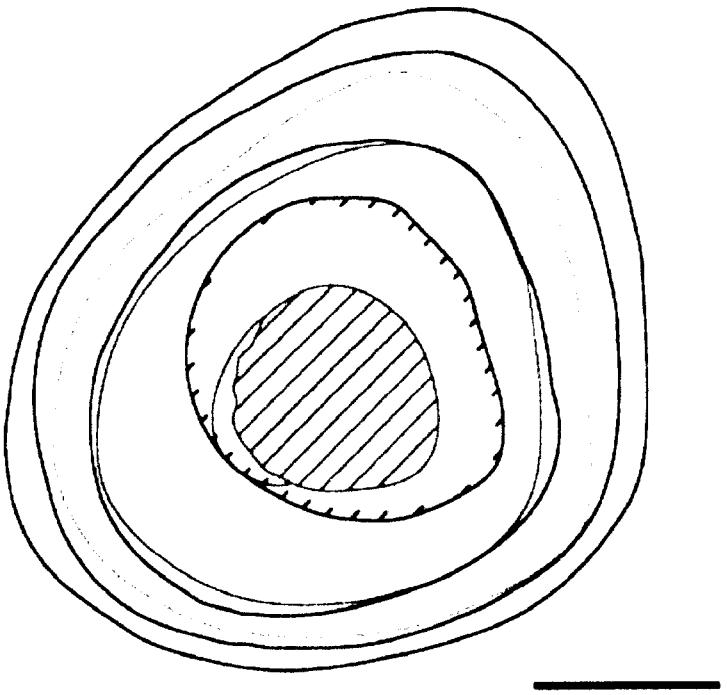

Figure 2.2 Result of superimposing line drawings showing the perimeters.

LAGs and medullary cavities of cross-sections through the tibiae of IVPP V14341.1 (brown, thick lines) and IVPP V14341.4 (green, thin lines).

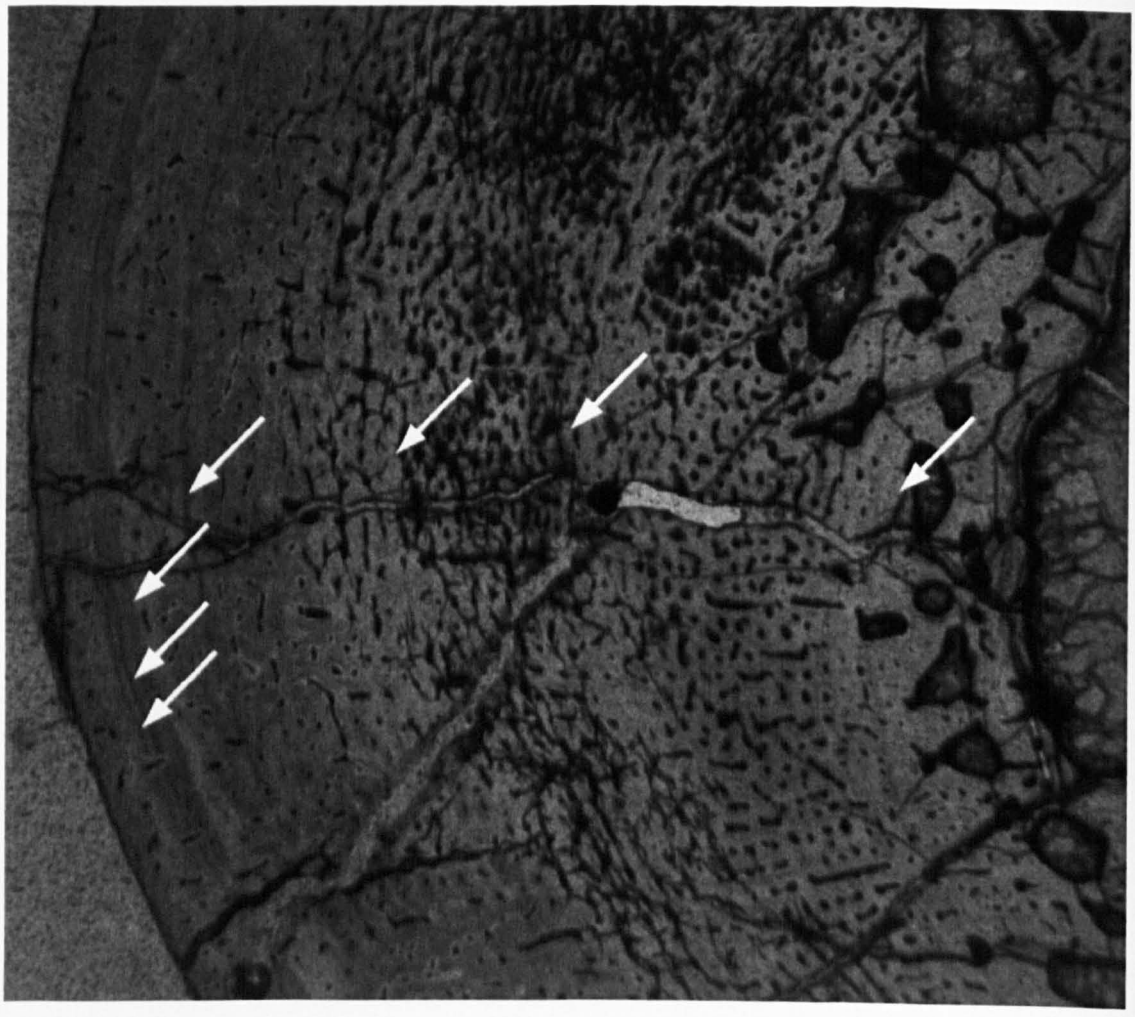

Figure 2.3 Transverse section through the humerus of an adult specimen of *Psittacosaurus lujiatunensis* (IVPP V12617)

Viewed under normal light to show LAGs (arrows).

There are seven LAGs in the humerus (Fig. 2.3). The diameter of the medullary cavity is 5.8 mm, exceeding the diameter of the third year LAG in the humerus of IVPP V14341.1 (5.3 mm). This indicates that the three innermost LAGs have been obliterated by the medullary cavity in the larger humerus, and that IVPP V12617 is a ten-year-old individual rather than a seven-year-old. Superposition of cross-sections through the two humeri confirms that three LAGs are missing in the larger one.

2.3 Vascular canal orientation

I classified vascular canals visible in the thin sections as longitudinal, radial or reticular (Chinsamy-Turan, 2005), and noted which canal types were present in each growth interval (i.e. interval bounded by LAGs) in each section. The relative numbers of the different canal types present were visually estimated. Provided that the medullary cavity had not expanded enough to destroy part of the record, a specimen with N LAGs could provide information about the vascularity of bone formed during the first year of growth ("first year bone"), and bone formed during all subsequent years up to N + 1. For example, a specimen with two LAGs could provide information about the vascularity of first year, second year and third year bone. Given that reticular and particularly radial canals are associated with relatively rapid deposition of bone, based on evidence from living birds (de Margerie et al., 2004), their presence was taken as an indication of rapid deposition in *P. lujiatunensis*.

2.4 Limb bone allometry

Coefficients of allometry were calculated for the lengths of the humerus, radius, ulna, tibia and fibula relative to that of the femur, following protocols used in earlier work by other researchers (Reisz et al., 2005), and for forelimb (humerus + radius) length relative to hindlimb (femur + tibia) length. The length measurements were log-transformed and then saved as a .txt file that could be read by the computer program R (R Development Core Team 2008). Each allometric coefficient was calculated in R based on a linear regression (using the lm command), with the slope of the regression line representing the coefficient. In all cases the 95% confidence interval for the slope excluded the isometric value of 1, indicating statistically

significant negative (for coefficients < 1) or positive (for coefficients > 1) allometry relative to the femur or hindlimb.

2.5 Numerical analysis in dinosarus

The diversity patterns among herbivorous dinosaurs (including ceratopsians) and plants during the Cretaceous are very interesting topics. Many hypotheses concern proposed interactions between herbivorous dinosaurs and early angiosperms during the Cretaceous period (Bakker 1978; Bakker 1986; Butler et al. 2009a; Tiffney 2004). Bakker (1978, 1986) proposed a link with the origin and early diversification of angiosperms. He considered that the shift from a high-browsing fauna (sauropods and stegosaurs) to a low-browsing fauna (ornithopods and ankylosaurs) created highly disturbed environments that favoured the evolution of the weedy, r-selected (i.e. high fecundity and short generation times) early angiosperms (Bakker 1978; Bakker 1986; Tiffney 2004). Other authors subsequently proposed that the middle to Late Cretaceous radiation of angiosperms might have driven the evolution and radiation of several herbivorous clades such as ornithopods, ceratopsians and titanosaurian sauropods (Barrett & Wills 2001; Coria & Salgado 2005; Tiffney 2004; Weishampel & Norman 1989). However, Lloyd et al. (2008) found few significant diversification shifts among dinosaurs in the Cretaceous, and one of only two was Neoceratopsia. Further, Butler et al. (2009a) argued that there are no clear changes in dinosaur diversity patterns during Hauterivian-Barremian (Early Cretaceous) that could be linked to the origin or early diversification of angiosperms. Furthermore, they considered that there is no significant spatiotemporal association between particular dinosaur groups and cycads (Butler et al. 2009b).

To test the diversity patterns in ceratopsians, I built a database comprising information on the global distribution of all ceratopsians. The database is collated from an extensive review of the primary literature, beginning with references cited in Weishampel et al. (2004) but also incorporating more recent references and data from The Paleobiology Database (http://www.paleodb.org). All the ceratopsians so far known, totalling 47 genera and 61 species, were involved in my database. And this is the first species-level analysis of ceratopsian diversity. Numerous analyses on diversity and numbers of formations will also be applied in my research to determine the bias of the fossil quality.

The character-based disparity of ceratopsians has not been studied in detail before. Disparity is the variance in morphology among organisms, and it may be assessed from continuous characters, such as measurements or landmarks that describe aspects of shape, or from discrete characters. There have been some disparity studies on ceratopsian skull shapes, based on landmarks (Chinnery, 2004; Dodson, 1993), and the only discrete-character study by Brusatte et al. (2012) is part of a wider study of dinosaurian morphological change through the Campanian and Maastrichtian.

Here, I explore discrete-character disparity, using the cladistic data matrix as the data source. These kinds of cladistic disparity studies have been carried out before on a variety of taxa, including arthropods (Wills et al., 1994), basal dinosaurs and temnospondyls (Brusatte et al., 2008a, b; Ruta et al., 2006), procolophonids (Cisneros and Ruta, 2010), ichthyosaurs (Thorne et al., 2011), and pterosaurs (Prentice et al., 2011; Butler et al., 2012). In all cases, there is clear evidence for decoupling (= separation) between diversity and disparity. Frequently, as was found also with continuous-character studies on disparity of marine invertebrates (Erwin, 2007), disparity generally expands first, diversity second in a diversification. This suggests

that a common evolutionary pattern is for organisms to explore the limits of possible shapes and forms, and then for new species to emerge that exploit the variance in morphology, but do not further expand the scope of that morphological diversity. In other words, the limits of morphospace are often exploited early, and later subclades tend to specialize into parts of the overall morphospace.

2.6 Methods in Phylogeny analysis

Valid ceratopsian taxa were determined from synoptic works (You and Dodson 2004; Dodson et al. 2004), updated from current literature, up to early 2012. These literature searches identified 61 valid ceratopsian species, including 31basal ceratopsians (*Chaoyangosarus*, psittacosaurids, and nonceratopsid neoceratopsians) and 30 valid derived ceratopsians (Centrosaurinae and Chasmosaurinae).

Phylogenetically informative characters were determined from all cladistic analyses on subsets of Ceratopsia performed since Sereno (1986). In the past 25 years, characters have been inherited from one analysis to the next, and new characters have been added, or older ones reformulated. The 318 characters come from Sereno (2000); Makovicky & Norell (2006); You & Dodson (2004); Ryan (2007); (Averianov et al., 2006); Xu et al. (2002); Chinney & Horner (2007); Dodson et al. (2004); Sampson et al. (2010); Farke et al. (2011); and Wu et al. (2007), respectively, and some are modified (Appendix I).

In compiling my master list of 318 unique characters, I listed all characters used before, organized them anatomically (from general skull features to details of the foot), noting the original sources and character numbers. Obviously synonymous

characters were combined and cross-referenced, and in cases of different formulations, the most recent wording of the character description was generally selected.

The complete matrix (Appendix II) comprises 318 characters and 62 taxa and was analyzed using the Heuristic search, with 10,000 random addition sequence replicates in PAUP* 4.0b10 (Swofford, 1998). All characters were parsimony informative, equally weighted, and considered unordered. Branches were collapsed if their minimum length equals zero, as such branches are not supported under all optimizations. Strict consensus methods were used to assay the commonality of branching patterns among all most parsimonious trees (MPTs). The taxa Pachycephalosauria was used as outgroup with trees rooted on the former according to current hypotheses of ornithischian relationships (e.g., Sereno, 1999).

Posterior to the analysis, the reduced consensus method of Wilkinson (1995, 2003) was applied in order to identify redundant taxa and unstable taxa, the deletion of which produced a more resolved strict (reduced) consensus tree. First, redundant taxa were identified and removed through 'safe taxonomic reduction' implemented using the program TAXEQ3 (Wilkinson, 2001b). Such redundant taxa have no unique combinations of character codings and are each identical to at least one other, more substantially coded, taxon in the analysis. Sych redudant taxa add nothing to the analysis, falling precisely on top of the identically coded taxon, but they do add many question marks and so extend the time of calculation and reduce the quality of the output. Secondly, so-called 'rogue taxa', forms that produce particular problems in a cladistic analysis, were identified. These may be taxa with limited codings but whose codings contradict everything presented by the other taxa. Their removal produces unexpectedly strong improvements in consistency index and other tree metrics, as

well as generally a much improved tree resolution. This technique was implemented using the 'strict' program of the REDCON 3.0 package (Wilkinson, 2001b).

2.7 Material and Methods in diversity analysis

To test the diversity patterns in ceratopsians, I built a database comprising information on the global distribution of all ceratopsians. The database was collated from an extensive review of the primary literature, beginning with references cited in Weishampel et al. (2004) but also incorporating more recent references and data from The Paleobiology Database (http://www.paleodb.org). All the valid ceratopsians so far known, totaling 49 genera and 62 species, were involved in mydatabase (see Appendix III). And this is the first species-level analysis of ceratopsian diversity. I summary the number of ceratopsian species present during each substages from Oxfordian to Masstrichtian to construct taxonomic diversity estimates (TDE, see Appendix IV). Use of stage subdivisions allows the identification of many short-term fluctuations in the diversity curves and provides a larger number of data points for statistical analyses (Barrett et al., 2009).

Phylogenetic diversity estimates (PDE) were generated based on the strict consensus tree in chapter 5, the unresolved clade were rearranged by the lasted published cladograms (Farke et al., 2011; Makovicky and Norell, 2006; Sampson et al., 2010; Sereno, 2010). Phylogenetic tree were constructed by plotting each species against time, allowing the inference of ghost lineages. I use a solution which were provide by Ruta et al. (2006) and Brusatte et al. (2008b) to calculate the branch length in the freely available statictical programming language R (http://www.graemetlloyd.com/methdpf.html).

To assess the influence of the rock record on ceratopsian diversity, I collected information on numbers of formations with ceratopsians. For the low quality of some geological sites, for example, the age of some formations are ambiguous or contain several stages, so I randomise my data by using programming language R to fit the unclearly dated formations to a fixed age. I compared the analysis with no random formations in which the ambiguous formation will fit each substages it contains.

2.8 Methods of disparity analysis

The dataset, which I used on the phylogenetic analysis, was used to derive a matrix of pairwise generalized Euclidean distances in MATRIX (Wills, 1998), which were then subjected to principal coordinates analysis (PCO, see Appendix V). The PCO analysis ordinated taxa into a taxon-defined morphospace, which is represented by three two dimensional plots of the first three axes in Figures 6.6, 6.7, and 6.8. Ordination was performed with the GINKGO software (Caceres et al., 2007), using the Cailliez method of negative eigenvalue correction. The PCO scores were used in disparity calculations using the software Rare (Wills, 1998). Twenty-one PCO axes were retained in calculations of disparity, and these explain cumulatively at least 50 per cent of the total variance in the data set. I divided the whole diversity of ceratopsians into four major groups: the most basal ceratopsians (including psittacosaurus and *Chaoyangosaurus*), basal neoceratopsians, centrosaruines, and chasmosaurines. For each group, I calculated mean and median values of disparity for two metrics, the sum of ranges and the sum of variances (Wills et al., 1994). The sum of ranges measures amount of morphospace occupation, whereas the sum of variances measures dispersal of taxa within a group, relative to the group's centroid (i.e., it

describes overall dissimilarity in terms of how far apart taxa are relative to their own mean configuration).

Chapter 3 Ontogenetic changes in the bone histology of *Psittacosaurus*

Author Contributions: This chapter has not previously been published. All material herein is the work of Q. Zhao

3.1 Ontogenetic bone tissue types in long bones of *Psittacosaurus lujiatunensis*

In this study, eighteen individuals of *Psittacosaurus lujiatunensis* from the Jehol Biota of China were histologically sampled, resulting in 43 thin-sections taken from the midshaft of, humeri, ulnae, radii, femora, tibiae and fibulae (see table 3.1). The sample, spanning a growth series from hatchling to adult developmental stages, was examined for life history and longevity estimates based on diaphyseal growth line counts and other features of histology. I recognized five different types of bone tissue.

	Humerus	Ulna	Radius	Femur	Tibia	Fibula	Age
IVPP V16902.1				0	0		<1
IVPP V16902.2	0			0			<1
IVPP V16902.3					0		<1
ELDM V1037					1		1
ELDM V1038.21	2	2		2	2		2
ELDM V1038.15					2	2	2
ELDM V1038.11	2	2		2	2	2	2
IVPP V14341.2					2	2	2
IVPP V14341.3					2	2	2
IVPP V14341.4					2	2	2

IVPP V14341.5					2	2	2
IVPP V14341.6	2	2	2				2
IVPP V14341.1	3			3	2 (1)	3	3
IVPP V14748				3 (2)	3 (2)		5
IVPP V14749	4 (1)			3 (2)	3 (2)		5
IVPP V18343						6 (1)	7
IVPP V18344						6 (1)	7
IVPP V12617	7(3)		5 (2)		8 (2)		10

Table 3.1 Numbers of LAGs in individual thin sections made during this study. Values in parentheses represent additional LAGs that are inferred to have been obliterated by expansion of the medullary cavity. An age estimate is given for each specimen, based on the evidence from all of the thin sections taken for that specimen. For IVPP V12617, the cross-section through the radius suggested a younger age (seven years) than cross-sections through the other sampled bones (ten years). However, only one juvenile radius was sectioned in my study, and it is possible that I have underestimated the number of LAGs obliterated by medullary cavity expansion in the radius of IVPP V12617.

Type A bone tissue is lamellar (or parallel-fibred) bone. The vascularization is mainly longitudinal and the density of the vascular canals is very high. The number of vascular canals has often been used as a proxy of the vascularization of the compacta (though this is not accurate, since Starck and Chinsamy (2002) have shown

that in juvenile modern bird bone only 20% of the channel is occupied by blood vessels). The vascular canals are large compared to those in the subsequent bone type B. Type A bone tissue normally has no laminar organization. Most of the osteocyte lacunae are oval and the long axis is parallel to the line of the osteocyte lacunae. No secondary osteons or LAGs are developed in type A bone tissue.

Type B bone tissue is fibrolamellar bone, but still with a high density of vascular canals. The vascular organizations are mainly longitudinal vascular canals (90%) with few reticular vascular canals (10%). The vascular canals are a little smaller (about 80% in diameter) than in type A. The greatest difference between type A and type B bone tissues is that in the developing primary osteons, the osteocyte lacunae start to line the vascular canals but they are still very simple, just one layer around the vascular canals, indicating that the primary osteon formation has started. Most osteocyte lacunae are round, but some of them are oval. The long axes of the oval osteocyte lacunae start to form a circumferential organization around the vascular canals. It is still too early to present secondary osteons or LAGs in this kind of bone tissue.

Type C bone tissue is primarily laminar fibrolamellar bone. More and more reticular vascular canals occur (nearly 35%). Also radial vascular canals can be observed (about 10%). The vascular organization compositions differ in the different limb bones. The density of vascular canals is also high in this type of bone tissue. The type C bone tissue is easy to distinguish from other types under polarized light. The type C bone tissue shows interlacing light banding under polarized light, while type B bone tissue shows flowing light banding. Most of osteocyte lacunae are elongate oval. Two or three layers of osteocyte lacunae surround the vascular canals to form the real

primary osteons. LAGs are present in type C bone tissue in their first appearance. No secondary osteons were observed.

In type D tissue, the lamellar bone becomes thicker. The vascularization is still high in type D tissue. The secondary osteons start to be present in the inner cortex, which is the greatest difference between types D and C. The vascular canals become smaller than in type C bone tissue. The osteocyte lacunae become a little more flattened than in type C bone tissue. LAGs are present in type D tissue evidently.

Type E bone tissue is fibrolamellar bone. The vascularization becomes decreased. The vascular canals are smaller than in type D bone tissue. The osteocyte lacunae become more flattened than in other bone tissue types, and the density is quite a bit lower compared to other bone tissue types. The density of secondary osteons between the erosion cavities is high.

3.2 Description of different ontogenetic stages of *Psittacosaurus lujiatunensis*

In the series of thin sections from *P. lujiatunensis*, I recognized four histological ontogenetic stages, i.e., hatchling, juvenile, sub-adult, and adult. None of the specimens was fully-grown.

3.2.1 Hatchling stage

The specimen IVPP V16902 is a cluster of hatchling *P. lujiatunensis* with five individuals (Fig. 3.1). These individuals are the smallest ones I have found. I made four thin sections from this cluster, including one humerus, two femora and one tibia.

Figure 3.1 IVPP V16902, the cluster of hatchling *P. lujiatunensis*

The humeral diaphyses of hatchling *P. lujiatunensis* primarily showed radial vascularization, although some simple reticular vascular canals were occasionally present (Fig. 3.2). Only very young "primary" osteons can be observed in the thin section, suggesting it is fast growing. No line of arrested growth (LAG) is present in the thin section. Type A bone tissue is the dominated tissue in the cortex.

The femoral thin section in the same individual showed only longitudinal vascular canals. It also just has primary osteons (Fig. 3.3). No LAGs or secondary osteons are present in this stage. Further, the dominant bone tissue is also type A bone tissue.

All these hatchling thin sections showed these individuals are all under one year old, because no LAGs can be found. Different bone tissues may imply different

growth rates. de Margerie (2002) found that laminar bone had significantly lower growth rates, while radial bone had significantly higher growth rates. Longitudinal and reticular bone had similar intermediate growth rates. So, comparing the radial vascular canals in the humerus and the longitudinal vascular canals in the femur, I considered that the humeri grew faster than the femora in the hatchling stage.

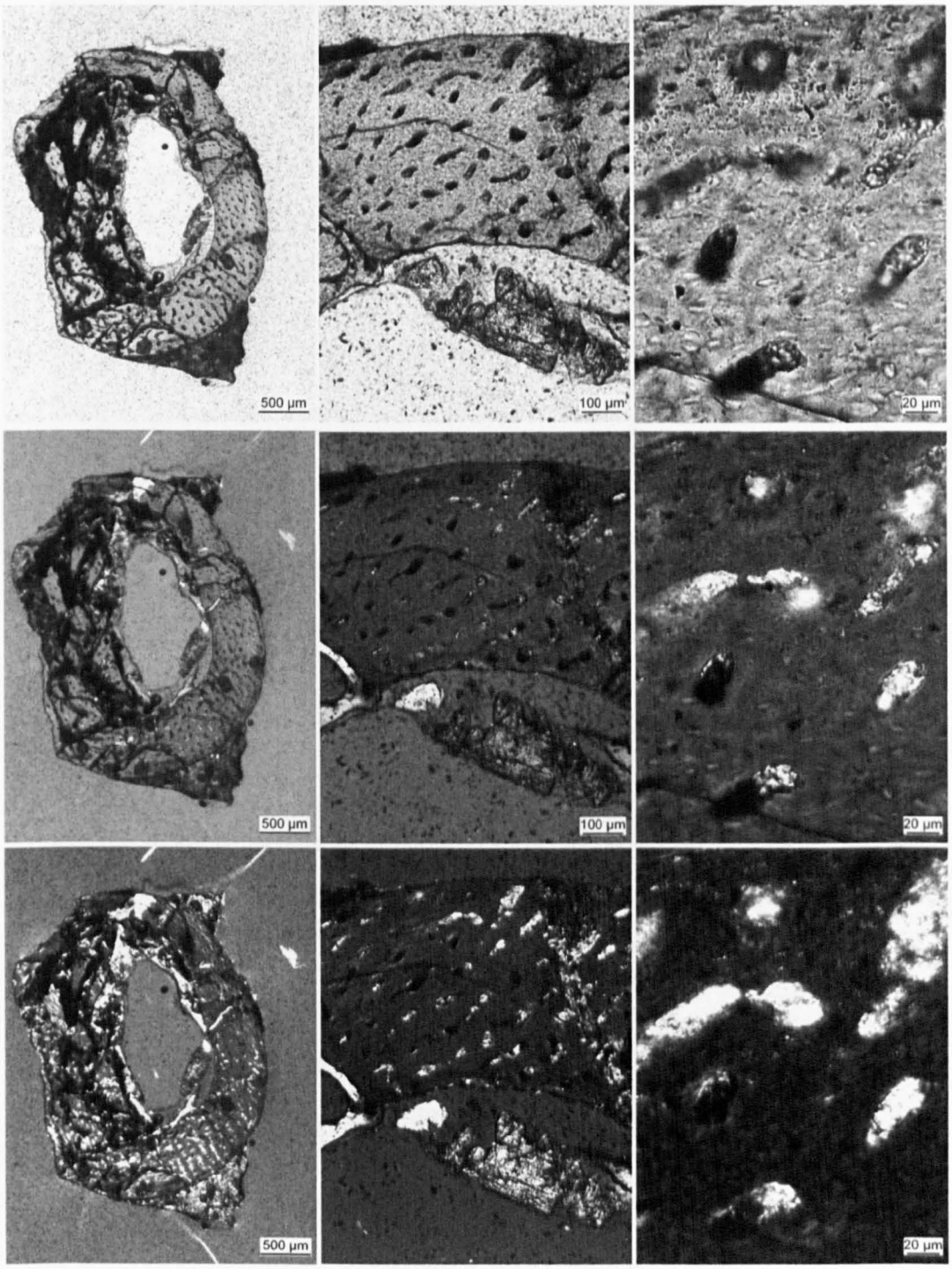

Figure 3.2 Mid-diaphyseal transverse section of a hatchling stage individual humerus, IVPP V16902.2

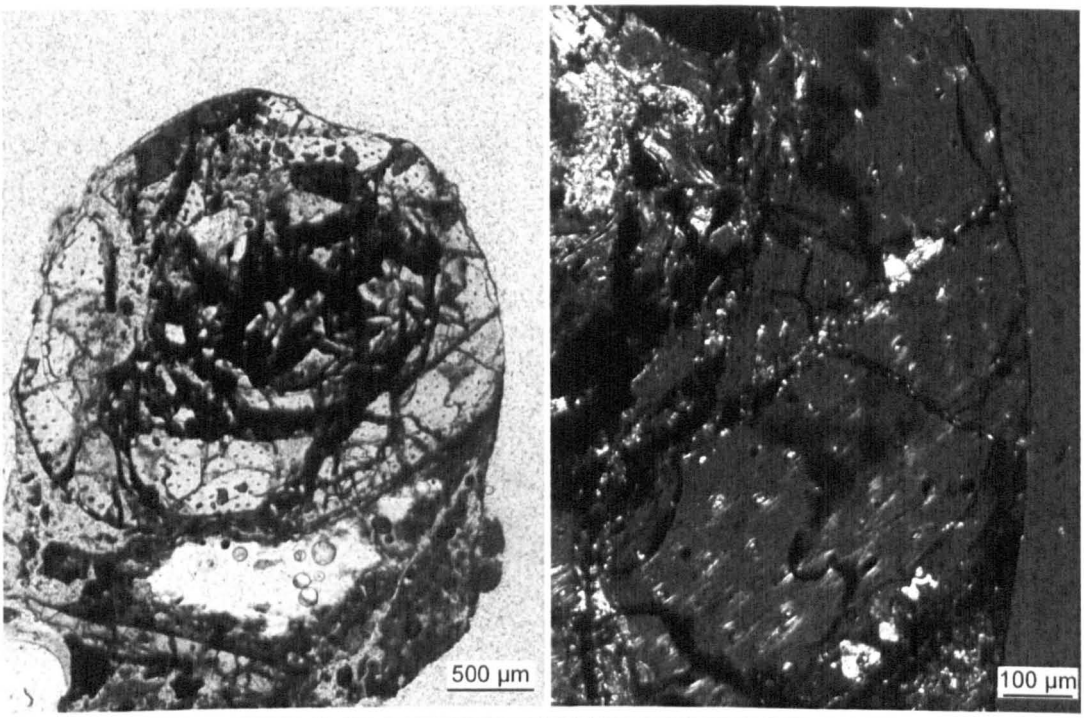

Figure 3.3 Mid-diaphyseal transverse section of a hatchling stage individual femur, IVPP V16902.2

3.2.2 Juvenile stage

The specimen IVPP V14341 is a cluster of juvenile *P. lujiatunensis* with six individuals (Fig. 1.1). I sampled all these six individuals to get the accurate ages. Two humeri, one ulna, one radius, one femur, five tibiae and five fibulae were taken from this cluster to make thin sections.

The biggest individual in this cluster is IVPP V14341.1 (Fig. 1.1). Thin sections of humerus, femur, tibia and fibula were taken from this individual. I found three LAGs in humerus, femur and fibula, but just two LAGs in the tibia. The medullary cavity must have absorbed the first-year LAG in the tibia. To test this, I took the other four tibial thin sections in different individuals of the same cluster. There are just two LAGs in each thin section. I drew each LAG on paper under the microscope, and then overlapped the pictures together. I found that the medullary cavity of the IVPP V14341.1 tibia is much bigger than the others, and its size overlaps the first-year LAG in the other tibiae. This strongly indicates that the first LAG had indeed been resorbed during growth.

The mid-diaphyseal transverse section of the fibulae showed three LAGs in IVPP V14341.1 (Figs. 3.4, 3.5), and two LAGs in the other four individuals (Figs. 3.4, 3.6, 3.7, 3.8, 3.9). The hind limbs of IVPP V14341.6 were in the rock, and would have been hard to take out. So I took the humerus, ulna and radius to make thin sections. All these thin sections from IVPP 14341.6 showed two LAGs, indicating that this individual was just two years old (Fig. 3.10). These have proved my previous

test in thin sections of tibiae. All the thin sections from this cluster obviously indicated that the small dinosaur specimens are offspring from two different clutches, each spaced about one year apart.

Horner et al. (1999) noticed that in a single skeleton of an individual dinosaur different bones may reflect different numbers of "growth rings" (= LAGs). This is probably because different bones in the skeleton have different morphology, and each requires specific remodeling processes, for example, a neural spine grows differently from a tibia (Chinsamy-Turan, 2005). In *Hypacrosaurus stebingeri* long bones, the tibia and the femur have eight growth rings, while the radius and fibula just have seven growth rings (Horner et al., 1999). I found a similar kind of variation in *Psittacosaurus lujiatunensis*, in the different numbers of growth rings in different long bones in IVPP V 14341.1, with two LAGs in the right tibia and three LAGs in the right femur and right humerus.

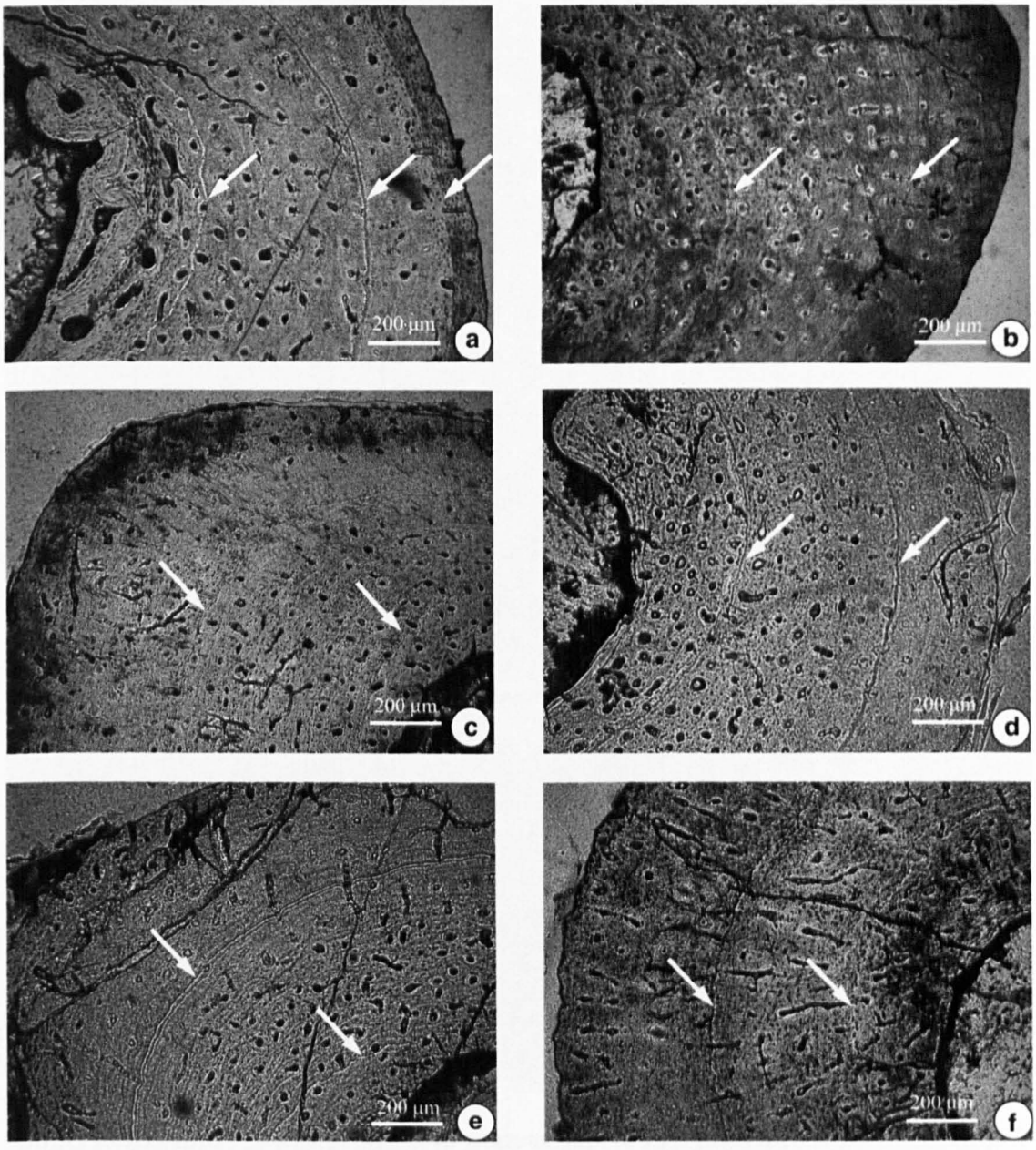

Figure 3.4 Mid-diaphyseal transverse sections of IVPP V14341

Five fibulae were taken from IVPP V14341.1 (Fig. 2.2a), IVPP V14341.2 (Fig. 2.2b), IVPP V14341.3 (Fig. 2.2c), IVPP V14341.4 (Fig. 2.2d) and IVPP V14341.5 (Fig. 2.2e). One radius was taken from IVPP V14341.6 (Fig. 2.2f). White arrows indicate LAGs. Numbers indicate identities of individual juvenile specimens, as shown in Figure 1.1.

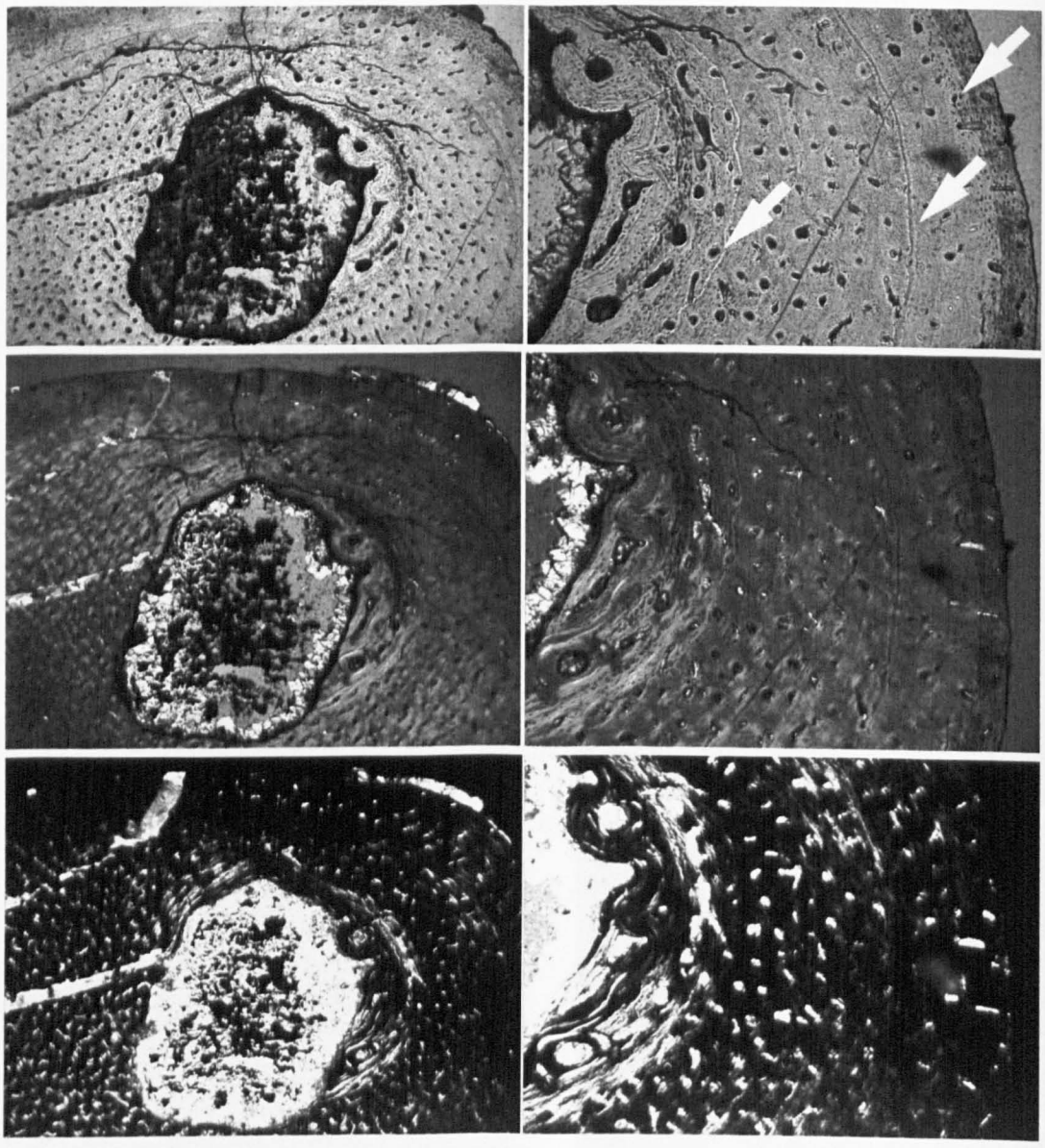

Figure 3.5 Mid-diaphyseal transverse section of a juvenile-stage individual right fibula (V14341.1),

Undering normal and polarized light. The arrow indicateds the LAGs.

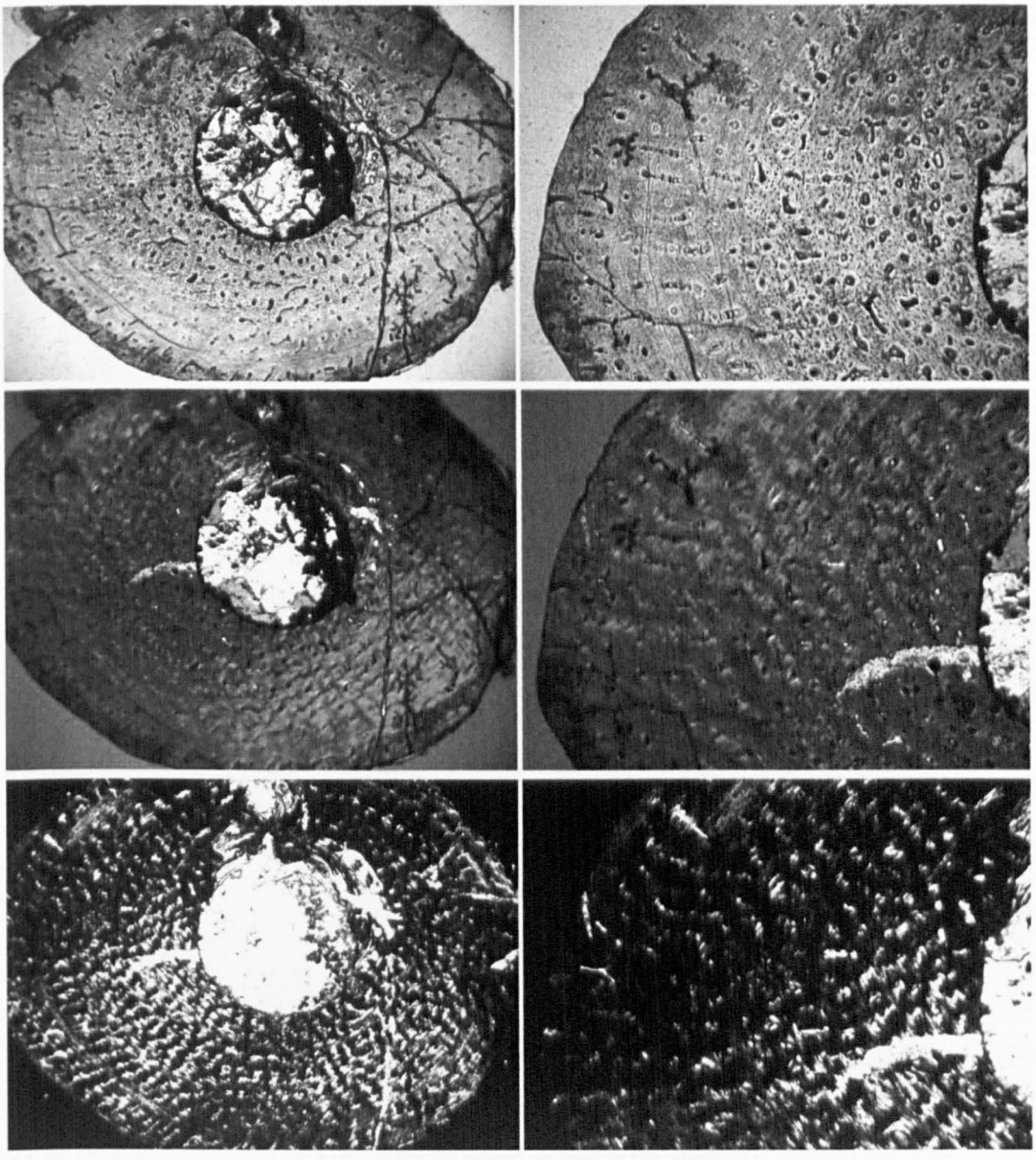

Figure 3.6 Mid-diaphyseal transverse section of a juvenile-stage individual right fibula, V14341.2

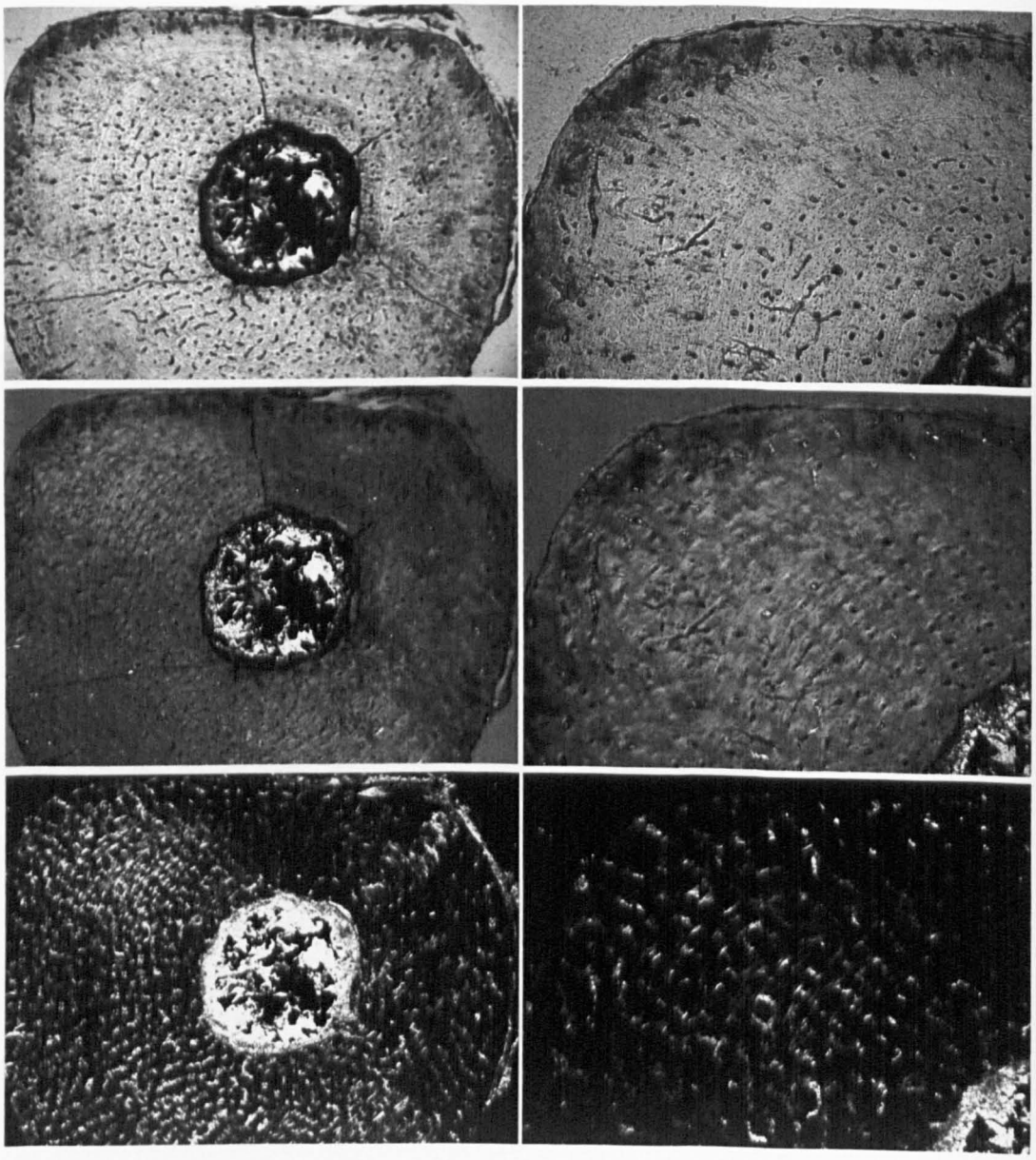

Figure 3.7 Mid-diaphyseal transverse section of a juvenile-stage individual right fibula, V14341.3

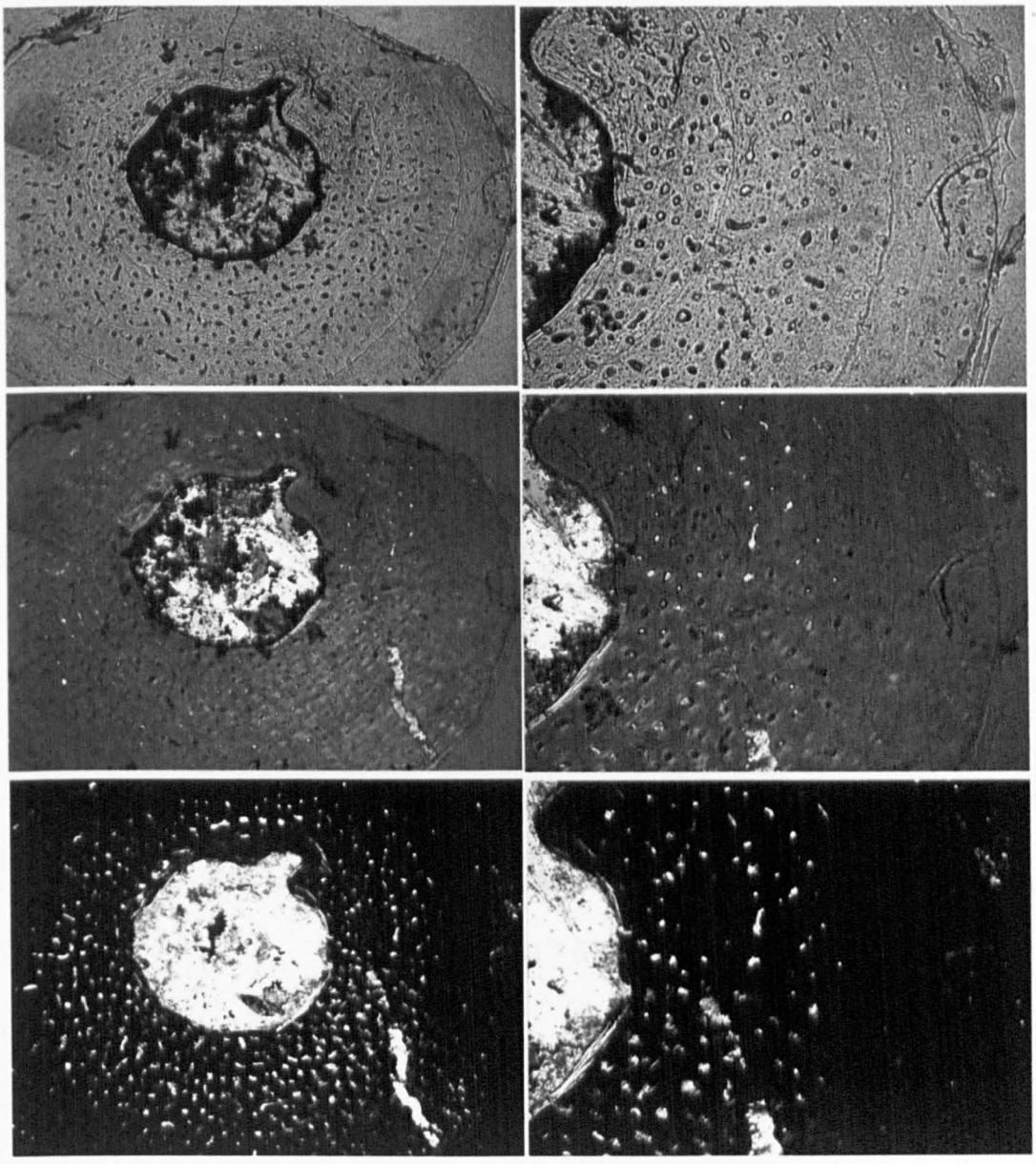

Figure 3.8 Mid-diaphyseal transverse section of a juvenile-stage individual left fibula, V14341.4

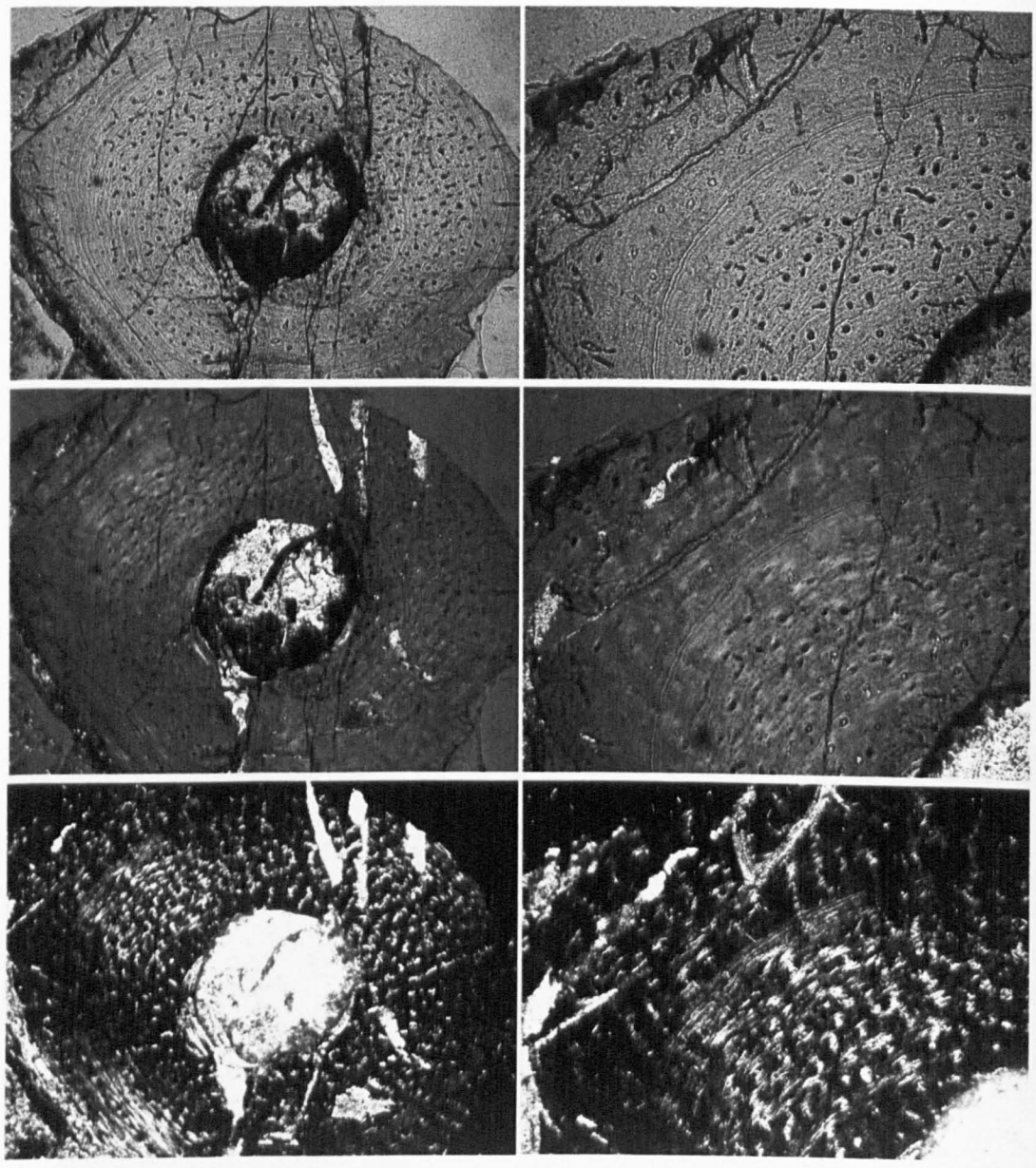

Figure 3.9 Mid-diaphyseal transverse section of a juvenile-stage individual left fibula, V14341.5

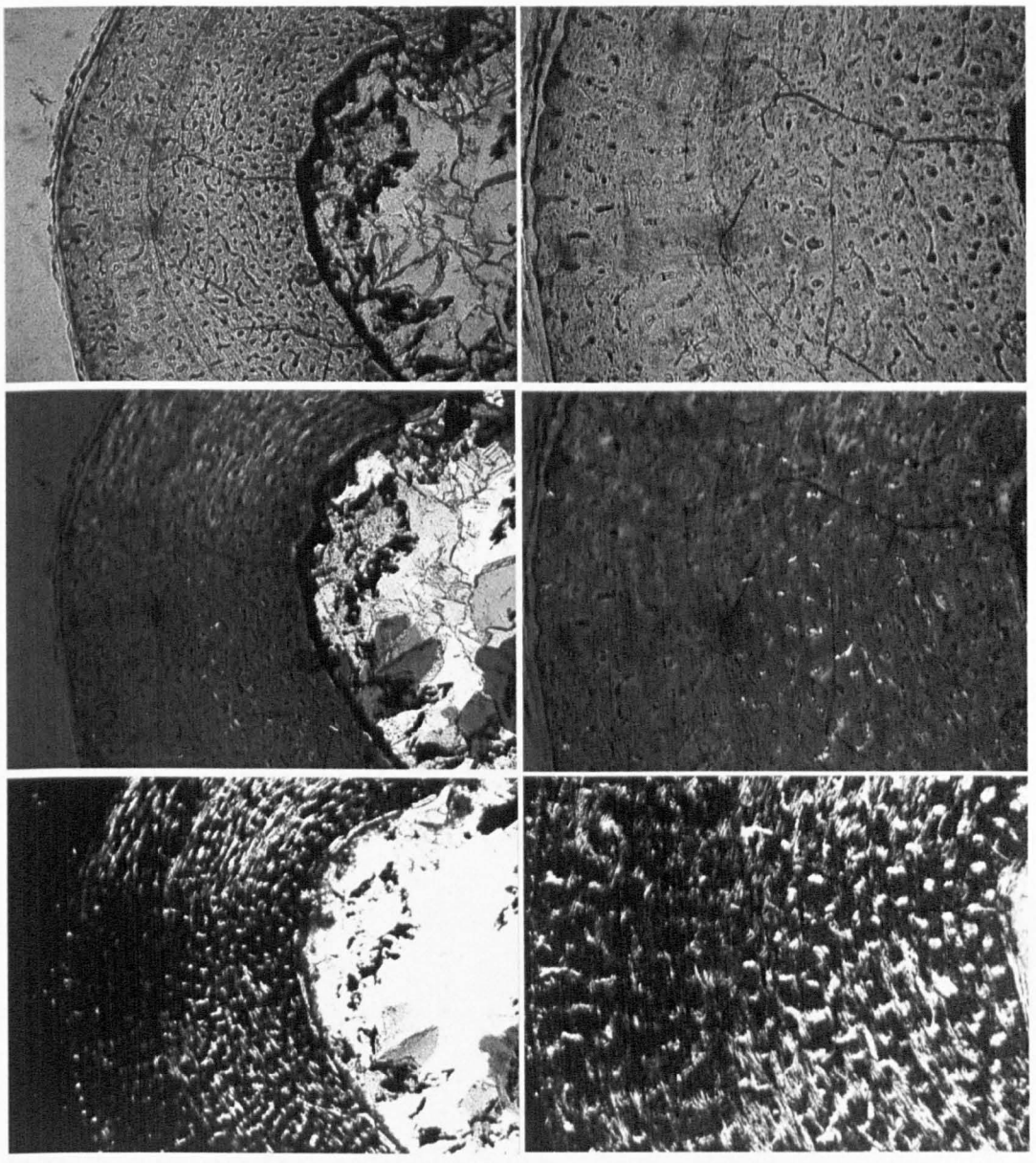

Figure 3.10 Mid-diaphyseal transverse section of a juvenile-stage individual right humerus, V14341.6

3.2.3 Sub-adult stage

The specimen IVPP V14748 is a very complete skeleton (Fig. 3.11). Tibia and fibula were taken to do the bone histology research. These two bones showed very different features in their vascular canals. The tibial diaphysis primarily showed reticular vascularization (Fig. 3.12), while the fibula was filled with longitudinal vascular canals (Fig. 3.13). Secondary osteons are present in the inner side of compacta of the tibia. All these features indicate that tibia had a much more faster growth rate than the fibula.

Both thin sections of tibia and fibula show three LAGs in the compacta. The medullary cavity expansion had effaced these two bones. One LAG has been absorbed by the medullar cavity. So the individual must passed its fourth year and entered its fifth year.

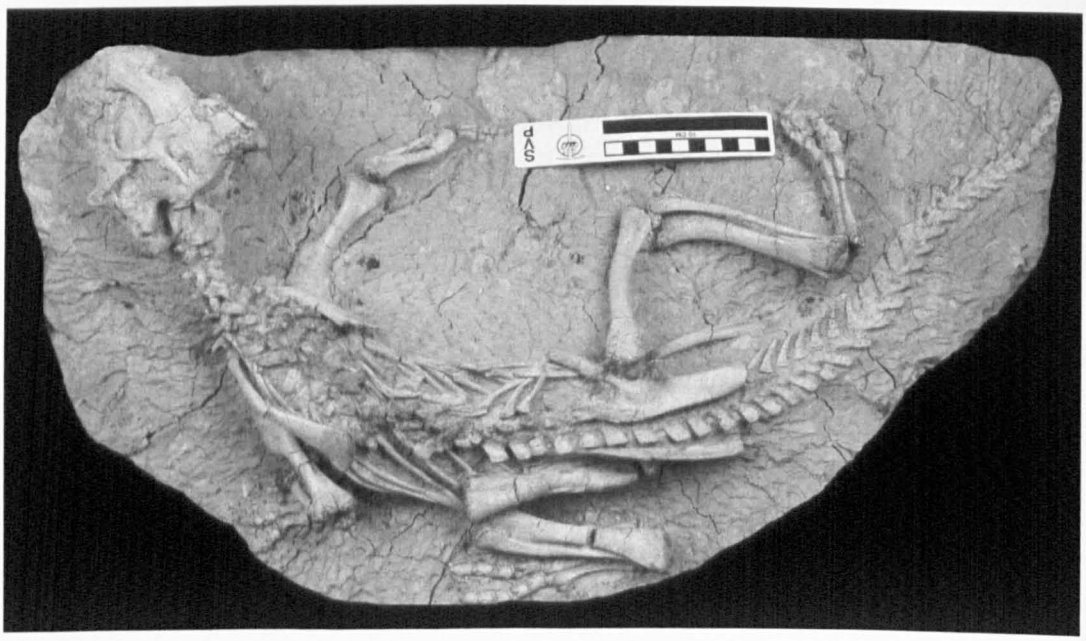

Figure 3.11 The skeleton of IVPP V14748 in sub-adult stage

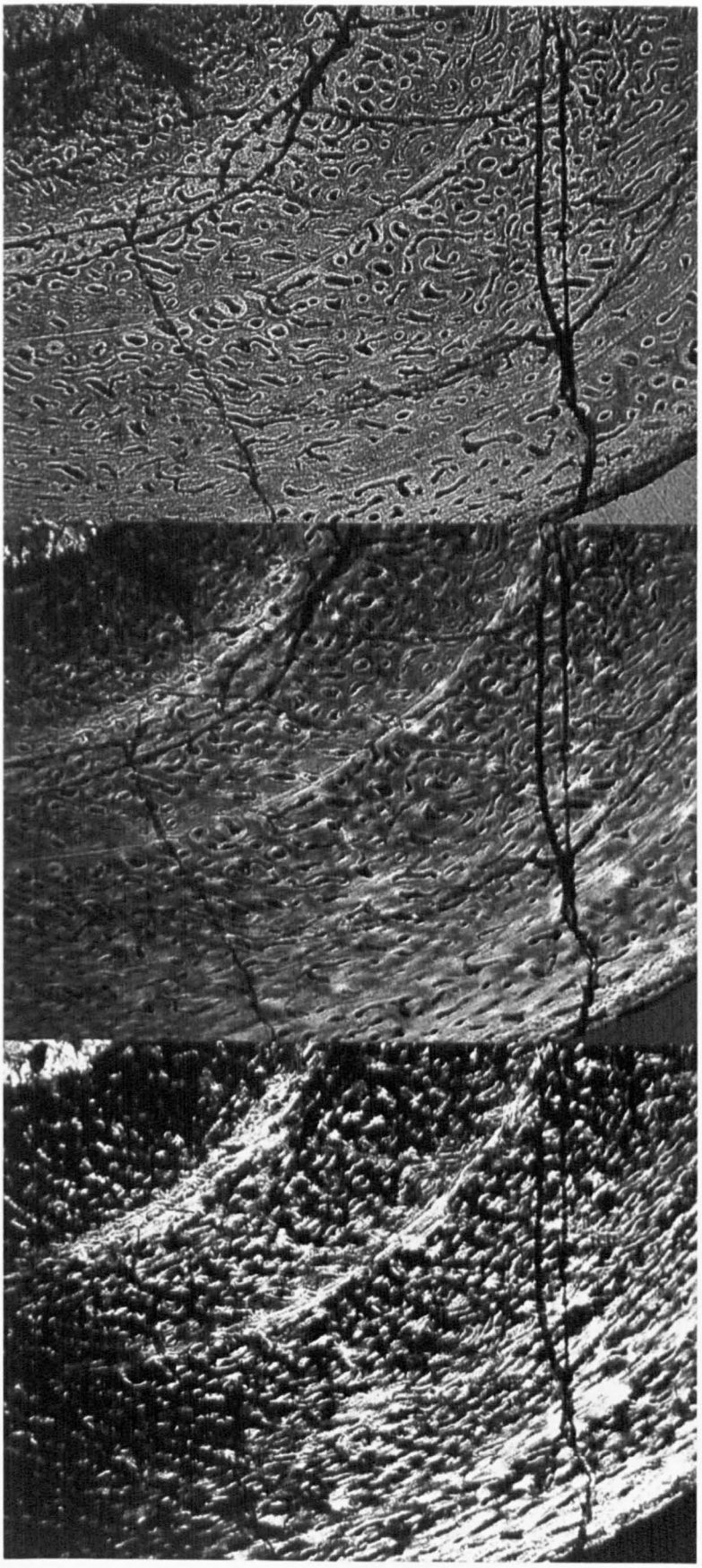

Figure 3.12 Mid-diaphyseal transverse section of a sub-adult stage individual left tibia, V14748

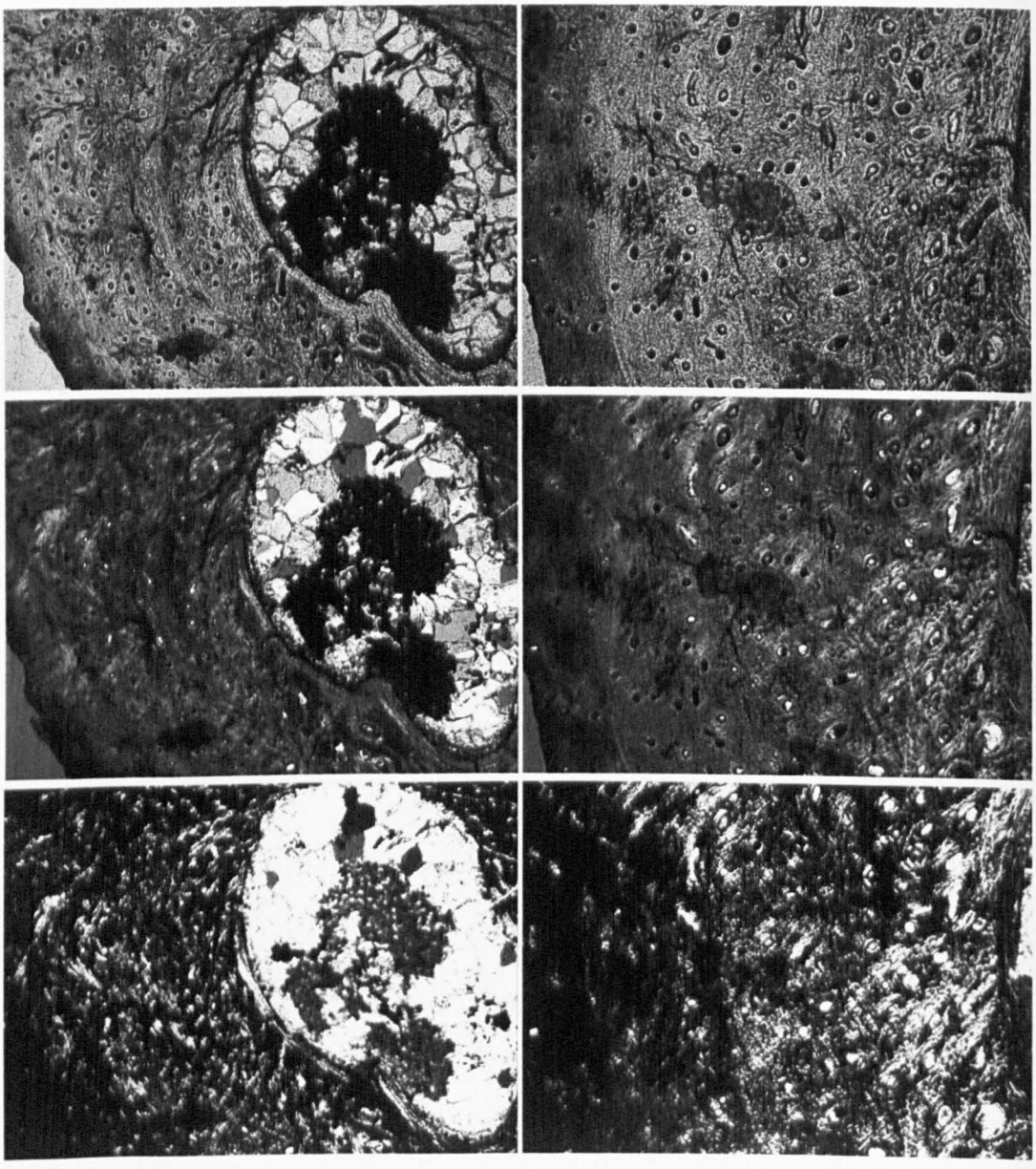

Figure 3.13 Mid-diaphyseal transverse section of a sub-adult stage individual left fibula, V14748

3.2.4 Adult stage

IVPP V12617 is an adult specimen. I took thin sections from the right tibia, radius and humerus. The longitudinal vascular canals and type E bone tissue dominate the thin section of right tibia and humerus. Eight LAGs were observed in the cortex but still no EFS (Fig. 3.14). The density of vascular canals is very low, which means the growth rate in this stage had become slow (Fig. 3.14). Many secondary osteons are observed. There are some primary osteons in the outer cortex (Fig. 3.14).

The vascular canal organization in the radius is different from other bones. Longitudinal vascular canals are still the main type in the inner cortex. In the middle cortex, there are some radial vascular canals. Just five LAGs are observed.

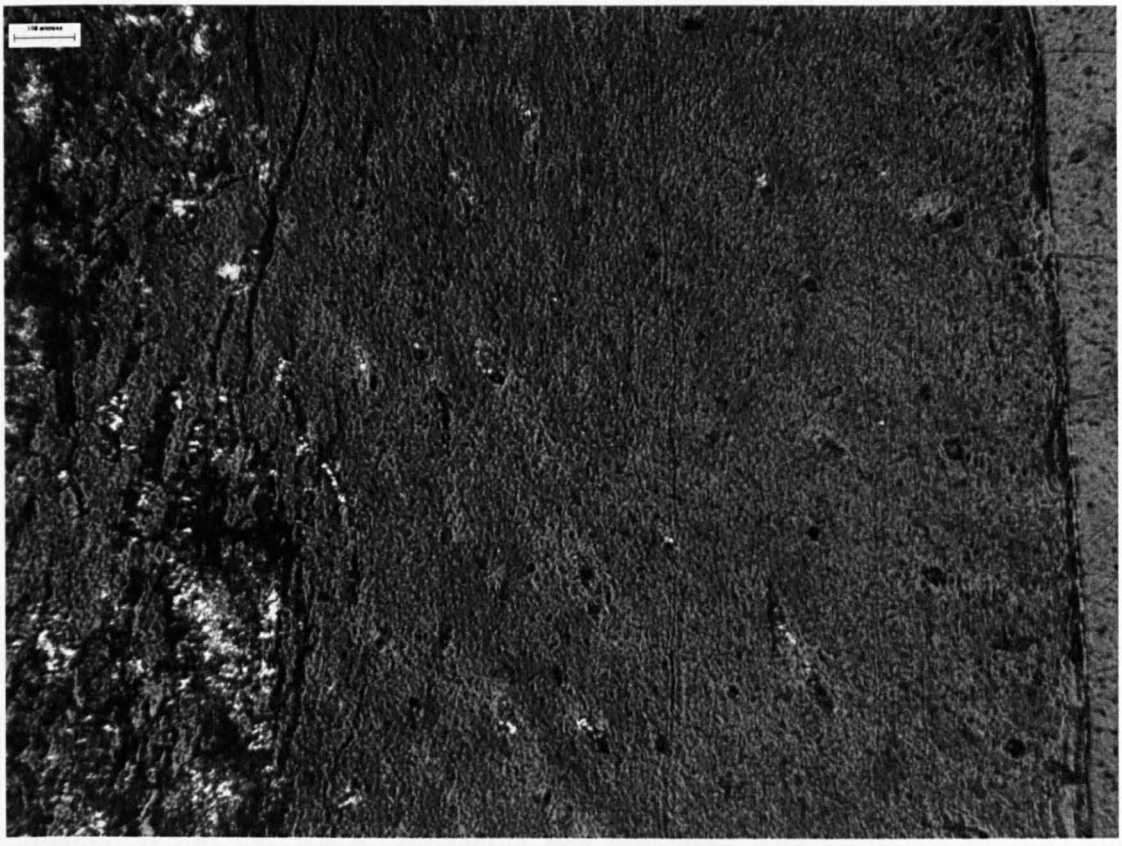

Figure 3.14 Mid-diphyseal transverse section of an adult stage individual tibia (IVPP V12617) under polarized light.

3.3 Conlusion of ontogenetic changes in bone histology of *P. lujiatunesnsis*

In this study, I recognized five different types of bone tissue and four ontogenetic stages. According to the density of vascular canals and the shape of osteocyte, I found the *P. lujiatunensis* grows faster in early stages (hatchling, juvenile, and subadult). The secondary osteons start to present in the subadult stage, which means the grow rate is slowing down. The dominant bone matrix in the long bones of *P. lujiatunensis* is fibrolamellar bone.

3.4 Differences in growth pattern between *P. lujiatunensis* and *P. mongoliensis*

The histological patterns observed in this study differ in some respects from those previously reported in a growth series of *Psittacosaurus mongoliensis* from the Lower Cretaceous of Mongolia sampled by Erickson & Tumanova (Erickson and Tumanova, 2000) (Fig. 3.15). The largest hindlimb bones (femur and tibia) in this growth series, representing individuals up to nine years old, show that radially vascularized fibrolamellar bone was deposited along part of the mid-shaft circumference beginning at the age of seven. Other parts of the mid-shaft circumference have only reticular or even longitudinal vascularization. This indicates that local apposition rate differed greatly along the circumference of the bone, presumably reflecting osseous drift (Erickson and Tumanova, 2000). One possible explanation for the occurrence of radial vascularization is a postural shift "from bipedality to quadrupedality" (Erickson and Tumanova, 2000), but this is unlikely given the strong evidence that adult individuals of *Psittacosaurus* were mainly bipedal (see below). The fitted growth curve for *P. mongoliensis* (Erickson and

Tumanova, 2000) indicates that at age 9 the largest sampled individuals had reached perhaps 80% of final body mass, a conclusion consist with the lack of an EFS in any of the sampled bones.

The largest histologically sampled individuals of *P. mongoliensis* thus appear to have been well short of their final adult size and still within the exponential phase of growth (Erickson and Tumanova, 2000), perhaps indicating that the presence of radial canals in the hindlimb bones simply reflects normal growth along a sigmoid curve of mass vs. age as in other dinosaurs including *P. lujiatunensis* (Erickson et al., 2009). However, the fact that the radial canals are limited to the hindlimb implies fast growth of the hindlimb relative to the forelimb at this stage of ontogeny, perhaps indicating a quadrupedal-to-bipedal postural shift like that inferred for *P. lujiatunensis* in the present study. However, radial canals were not observed in any of the hindlimb bones that I sectioned, suggesting that their occurrence in *P. mongoliensis* represents either a genuine difference in growth pattern between the two species or a result of pathology (Erickson and Tumanova, 2000).

The largest *P. mongoliensis* femur sampled was 210 mm long, representing a nine-year-old animal that had still not reached maximal body size as mentioned above. By contrast, the largest known *P. lujiatunensis* femur measures 202 mm (Erikson et al. 2009), and must have been close to final size because the largest femur sampled in the present study is only about 160 mm long but appears almost fully grown on the basis of histology. This femur represents an individual (IVPP V12617) that I consider to be ten years old on the basis of histology, although it was previously interpreted as a six year old on the basis of femur size alone (Erickson et al., 2009).

Femur length comparisons informed by histology suggest larger adult body size in *P. mongoliensis*, but inferred growth curves for the two species (Erickson et

al., 2009; Erickson and Tumanova, 2000) show a considerably higher mass for *P. lujiatunensis* than for *P. mongoliensis* (38 kg in the former vs. 25 kg in the latter). There are several possible solutions to this paradox, including the fact that the mass estimates used to construct the growth curves were based on circumference rather than length measurements (Erickson et al., 2009; Erickson and Tumanova, 2000), but it can only be solved by an analysis directly comparing the two species in terms of both histology and skeletal proportions. I note, however, that both logistic growth curves extrapolate well beyond the available histological data, and I therefore prefer the direct histological and meristic evidence suggesting that *P. mongoliensis* grew to a larger final size than *P. lujiatunensis*.

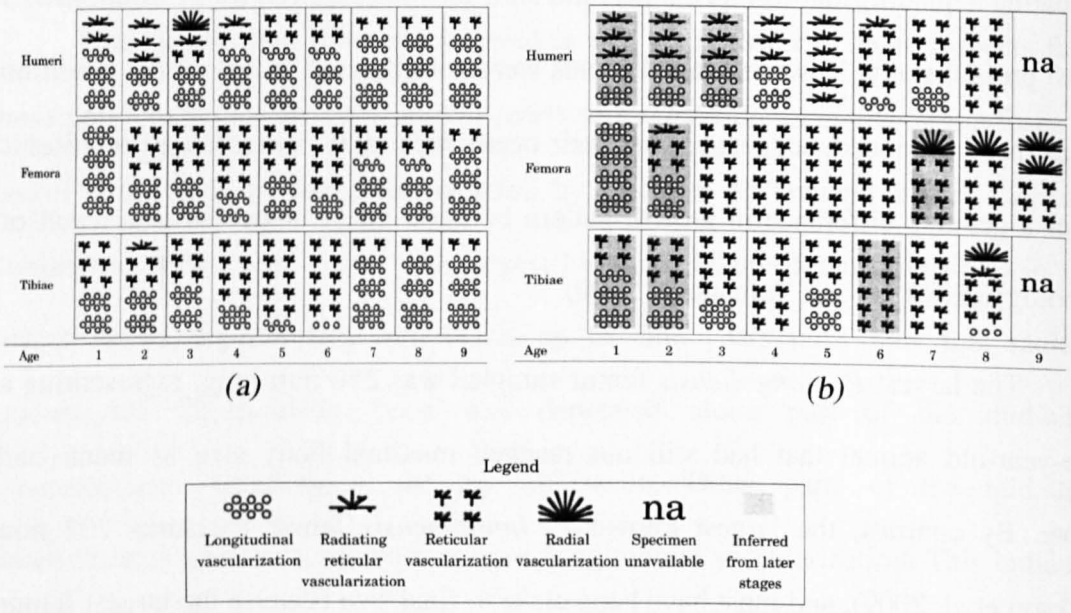

Figure 3.15 Diagram depicting changes in diaphyseal vascularization patterns during ontogeny for various major long bones in *P. lujiatunensis* (a) and *P. mongoliensis* (b)

The icons within each rectangle represent vascular canal branching patterns prevalent in each respective thin section that were deposited during the last 'annual' bout of bone deposition.

Chapter 4 Histological evidence for timing of a postural shift during the early growth of ceratopsian dinosaur

Author Contribution: This chapter has been accepted for publication in the journal *Nature Communications*:

Zhao, Q., Benton, M. J., Sullivan, C. Sander, M. P., and Xu, X. Histological evidence for timing of posture shift during early growth of ceratopsian dinosaurs

This study built upon the initial PhD project outline as written by M. J. Benton. Discussion with M. J. Benton, X. Xu, and M. P. Sander, who aslo reviewed and edited the manuscript during preparation, Q. Zhao is the lead and corresponding author of this paper and has contributed all of the work in analysing the data and preparing the manuscript.

4.1 Introduction

A few dinosaurs are inferred to have undergone an ontogenetic shift from quadrupedal to bipedal posture, or vice versa, based on skeletal allometry. The basal ceratopsian Psittacosaurus lujiatunensis is considered to have been mainly bipedal as an adult. Here I want to infer a postural shift in this species based on a novel combination of limb measurements and histological data. The allometric relationship between the forelimb and hindlimb will be discussed in the chapter. Bone histology information will also be used to indicate the growth rate in different individuals. Histology also makes it possible to determine the ontogenetic ages of individual specimens, showing that the forelimb-to-hindlimb ratio changed rapidly during the first year or two of life and thereafter decreased gradually. Occurrence of an ontogenetic shift from quadrupedality to bipedality was evidently widespread in dinosaurs, and may even represent the ancestral condition for the entire group.

4.2 Results

4.2.1 Dinosaur age profiles

One of the specimens (IVPP V14342) in the data set was unavailable for histological sampling, but for every other individual I took histological sections from the humerus, radius, ulna, femur, tibia and/or fibula. Across all individuals, a total of 41 bones were sectioned in this analysis.

Three of the individuals were from a cluster (IVPP V16902) of very small juveniles, and sectioning their long bones revealed no lines of arrested growth (LAGs). Accordingly, they appear to have been hatchlings less than one year old at

the time of death, and they probably represent the smallest *Psittacosaurus* specimens ever reported (femur lengths 22 and 26 mm). The other individuals in the sample were at least one year old. Of the six skeletons from the cluster IVPP V14341, five were found to be two years old whereas the sixth was found to be three years old (Figure 3.4), indicating slight heterogeneity in the ages of the individuals in this apparent social group. Four of the individuals were from another cluster (ELDM V1038, Fig. 4.1), and were all found to be two years old. All of the individuals in the data set that were preserved in isolation (rather than as part of a cluster) and could be studied histologically were at least five years old and ranged in age up to ten years old (Table 4.1), although the single isolated skeleton (IVPP V14342) that could not be studied histologically was close in size to the three-year-old in cluster IVPP V14341. Conversely, all the specimens in clusters that were studied histologically were three years old or younger.

Figure 4.1 Cluster of juvenile *Psittacosaurus lujiatunensis* specimens (ELDM V1038).

Scale bar is 10 cm.

4.2.2 Limb allometry

Length measurements from *P. lujiatunensis* long bones demonstrate that the humerus, radius and ulna are negatively allometric relative to the femur, with allometric coefficients of 0.89, 0.72 and 0.78 respectively (Tables 2.2 and 2.3, Figure 2.4). The growth of the tibia and fibula relative to the femur is statistically distinguishable from isometry, but the coefficients (0.97 and 0.94, respectively. Tables 4.2 and 4.3, Figure 4.2) indicate only minimal negative allometry. The tibia remained slightly longer than the femur (averaging 110% of femoral length across the entire sample) throughout ontogeny. As a whole, the forelimb became shorter relative

to the hindlimb over the ontogeny of an individual *P. lujiatunensis*, the allometric coefficient of forelimb length relative to hindlimb length being 0.83. In the three hatchling (< 1 year old) individuals the forelimb-to-hindlimb ratio (the ratio of the combined length of the humerus and radius to that of the femur and tibia) averaged 0.84. The ratio averaged 0.70 in one-year-olds, but thereafter decreased gradually and steadily to an average value of 0.61 in seven-year-olds. The single ten-year-old specimen had an anomalously large ratio of 0.66, suggesting that this individual had unusual proportions. The anomaly might be taken as evidence supporting the original referral of this individual to *Hongshanosaurus houi* (You and Xu, 2005), but other aspects of this specimen's morphology still make a strong case for assigning it to *P. lujiatunensis* instead (Sereno, 2010; Zhou et al., 2006b).

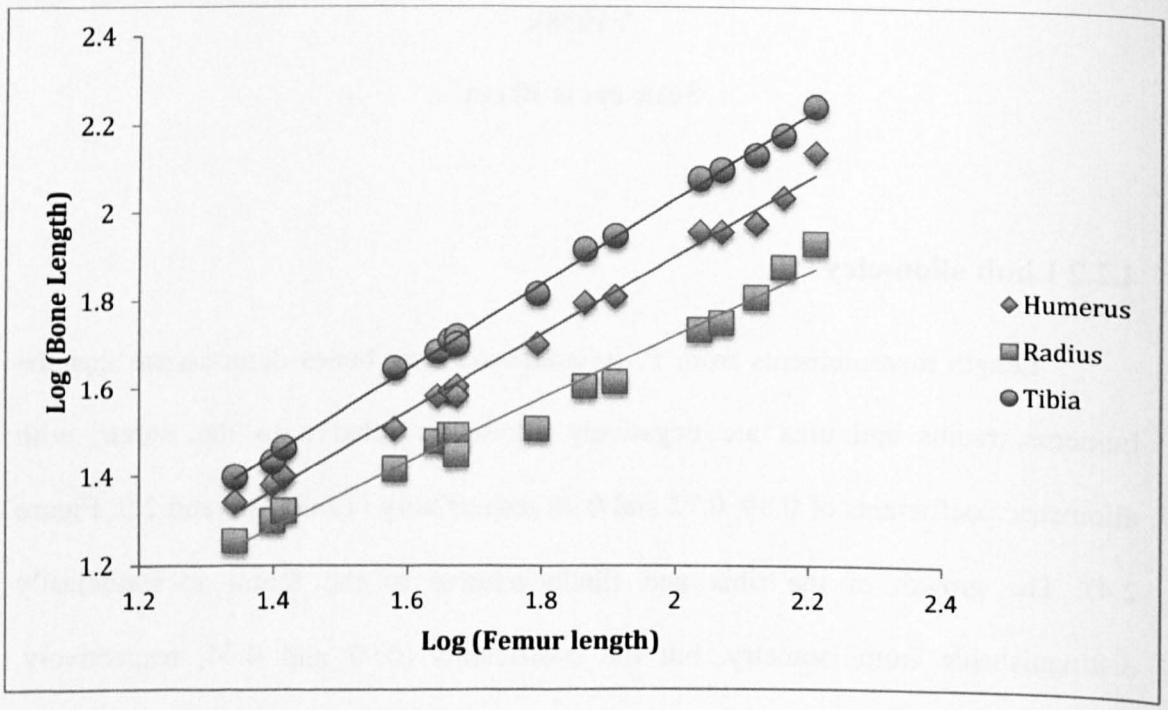

Figure 4.2 Relative growth in the appendicular skeleton of *Psittacosaurus lujiatunensis*

Based on a regression analysis□ of the lengths of the humerus, radius and tibia relative to that of the femur. Measurements of the ulna and fibula were very similar to those of the radius and tibia, respectively, so the ulna and fibula were omitted from the graph for the sake of clarity.

4.2.3 Bone histology

The thin sections of the 41 bones included in the histological analysis reveal many important details of vascular canal orientation and other aspects of microstructure. In all sections, the cortex is composed of fibrolamellar bone. The degree of vascularization is high in early growth, but appears to decrease relatively abruptly beginning at the age of four or five. Similarly, only primary osteons are present in the younger individuals in the data set, but secondary osteons are visible in the long bones of all specimens that are at least five years old. Only the largest specimen in the data set shows evidence of remodelling of the secondary osteons.

The forelimb and hindlimb bones show different patterns of canal orientation during ontogeny, although only limited information is available for the radius and ulna. Throughout most of ontogeny a combination of reticular and longitudinal canals is present in the humerus, the proportion of reticular canals being higher during the earlier half of growth and reaching a maximum in second-year bone (i.e. bone deposited during the second year of life, between the first and second LAGs). In third-year bone both radial and reticular canals, as well as longitudinal ones, are present (Fig. 4.3a). These patterns suggest that bone was deposited rapidly during the early growth of the humerus, but that the rate of deposition decreased in later ontogeny. For the radius and ulna, good histological evidence is available only for the first three years of growth, but bone formed during this period also shows a relatively high

proportion of reticular canals in these elements. In the radius, third-year bone also contains radial canals, as in the humerus (Fig. 4.3b). The evidence based on canal orientation from the entire forelimb suggests rapid deposition of bone, consistent with the presence of a high level of vascularization during early growth.

Patterns of canal orientation in the hindlimb, however, are strikingly different. No hindlimb section shows the presence of radial canals at any stage of growth (Figs 2.3 and 4.3), and the proportion of reticular as opposed to longitudinal canals is highest in bone formed during middle (between the ages of approximately three and six) rather than early ontogeny (Fig. 2.3c,d). The middle period of growth can therefore be identified as the time when bone was being deposited most rapidly in the hindlimb.

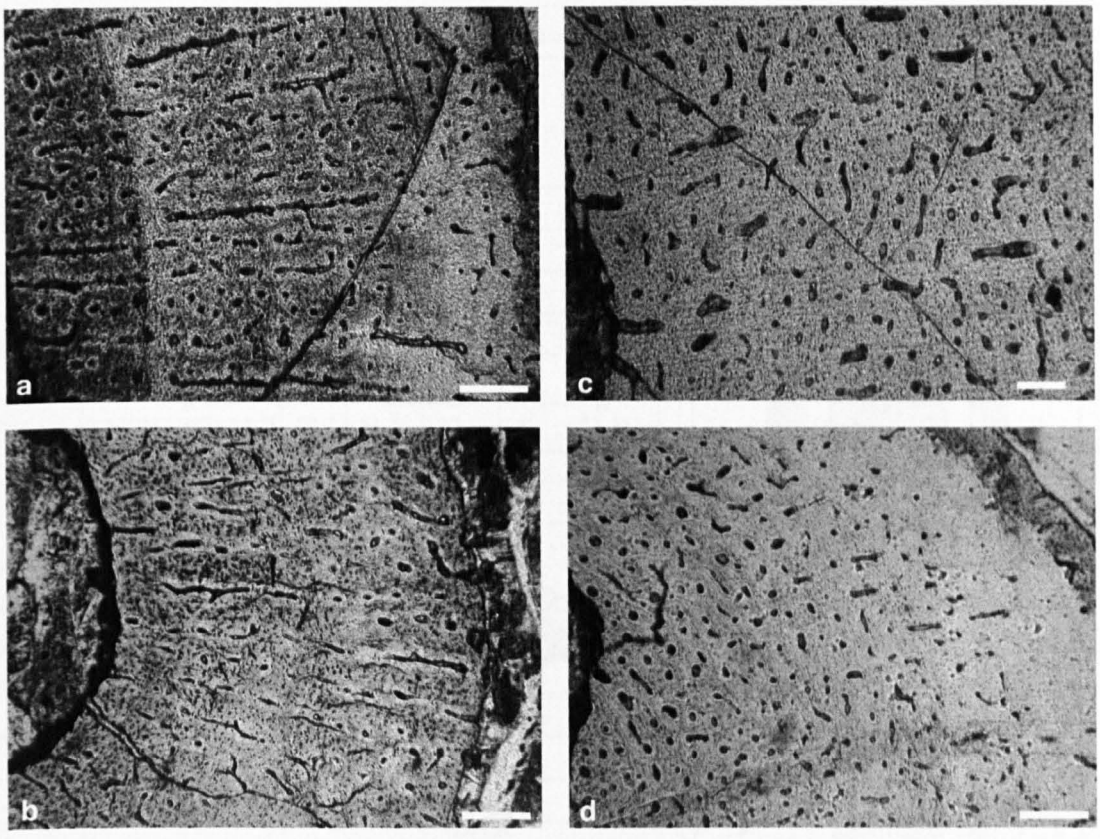

Figure 4.3 Histological thin sections through bones of the forelimb and hindlimb of juvenile *Psittacosaurus lujiatunensis* in normal light.

The thin sections are taken transversely across entire sections of the humerus (**a**), radius (**b**), femur (**c**) and fibula (**d**) of a 2-year old (**b**) and the three-year-old (**a**, **c**, **d**). Scale bars in each image are 200 μm.

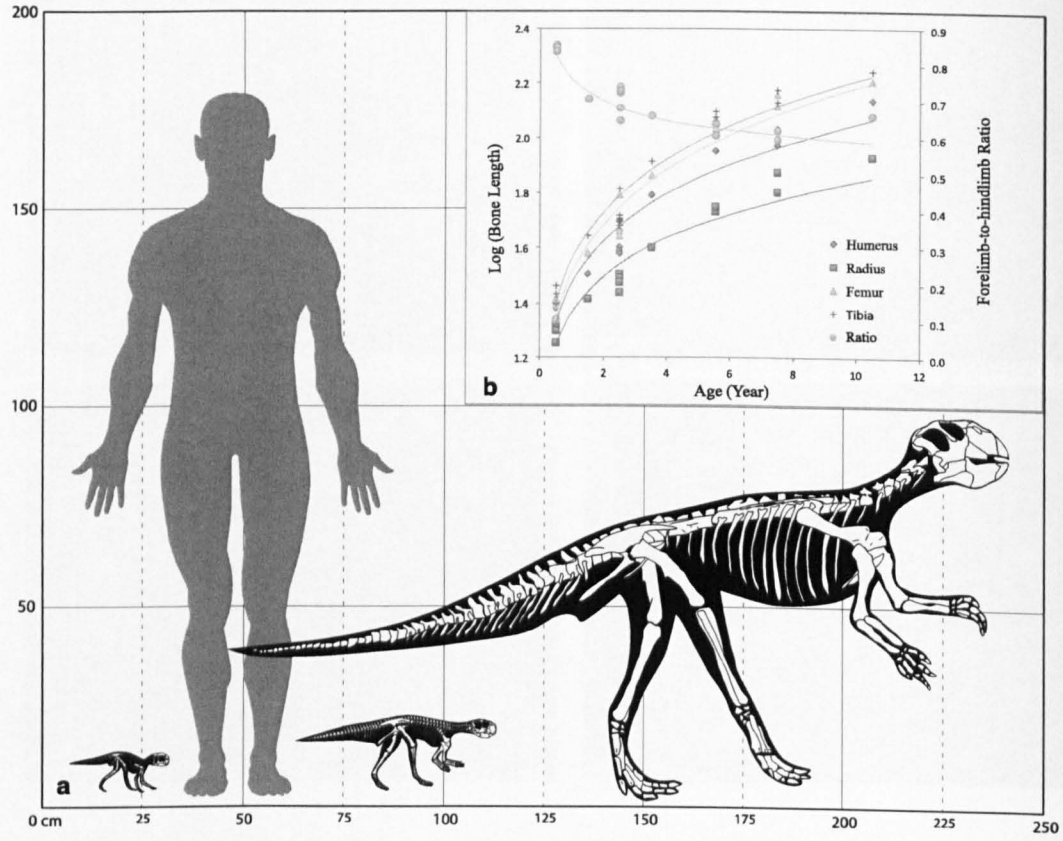

Figure 4.4 Growth and postural change in *Psittacosaurus lujiatunensis*.

(a) Skeletal reconstructions of hatchling, juvenile and adult individuals showing inferred postural change, with 178-cm-tall man for scale. (**b**) Graph showing uneven length increase in various long bones, and changing value of the forelimb-to-hindlimb ratio, as a function of age in years. Forelimb elements increase in length more slowly than hindlimb elements, resulting in decreasing forelimb-to-hindlimb ratio and increasingly bipedal posture as growth continues. Long bone measurements indicate the forelimb-to-hindlimb ratio changes most rapidly during early growth

	Specimen number	Humerus	Radius	Ulna	Femur	Tibia	Fibula	Forelimb	Hindlimb	Forlimb/ Hindlimb Ratio	Age
Hatchling	IVPP V16902.1	22	18	18	22	25	24	40	47	0.851	<1
	IVPP V16902.2	24	20	20	25	27	25	44	52	0.846	<1
	IVPP V16902.3	25	21	21	26	29	30	46	55	0.836	<1
Juvenile	ELDM V1037	32	26	28	38	44	48	58	82	0.707	1
	ElDM V1038.21	38	30	32	44	48	53	68	92	0.739	2
	ElDM V1038.15	39	31	30	46	51	54	70	97	0.721	2
	ElDM V1038.11	40	31	31	47	52	56	71	99	0.717	2
	ElDM V1038	38	28	30	47	50	52	66	97	0.680	2
	IVPP V14341.4	50	32	35	62	65	70	82	127	0.646	2
	IVPP V14341.1	62	40	42	73	82	82	102	155	0.658	3
	IVPP V14342	64	41	44	81	88	89	105	169	0.621	?
Sub-adult	IVPP V14748	90	54	59	109	119	118	144	228	0.633	5
	IVPP V14749	90	56	65	117	125	122	146	242	0.604	5
	IVPP V18343	94	64	74	132	135	135	158	267	0.592	7
	IVPP V18344	108	75	75	145	150	149	183	295	0.620	7
Adult	IVPP V12716	137	85	94	162	175	165	222	337	0.659	10

Table 4.1 *Psittacosaurus lujiatunensis* specimen length measurements in mm; raw data used in Figure 2.3.

Numbers indicate identities of individual juvenile specimens, as shown in Figure 1. All specimens are from the Lujiatun locality and share the same age, facies, and location information.

Length 1	length 2	slope	S
Humerus	Femur	0.885	0.022
Radius	Femur	0.724	0.030
Ulna	Femur	0.775	0.026
Tibia	Femur	0.969	0.011
Fibula	Femur	0.944	0.026
Forelimb	Hindlimb	0.834	0.021

Table 4.2 Allometric coefficients (slopes) and standard error values from regressions of limb measurements.

Length 1 and Length 2 are lengths of either bones or limbs. In each case, Length 1 was regressed against Length 2 with both variables log-transformed. The Slope from the linear regression represents an allometric coefficient, and the S value represents the standard error associated with the slope.

4.3 Discussion

4.3.1 Histology and bone growth

The observed changes in vascular canal orientation during the growth of particular long bones suggest shifts in the rate of bone deposition that may correlate with postural changes. This line of evidence indicates that deposition of bone was most rapid during early ontogeny in the case of the forelimb bones. In the humerus, at

least, growth appears to have slowed following deposition of the third LAG. In the hindlimb bones, by contrast, growth appears to have been most rapid during the fourth through sixth years of life. Unfortunately, histology does not provide a basis for directly comparing rates of bone deposition between the forelimb and the hindlimb. However, the fact that the forelimb appears to grow most rapidly during early ontogeny, whereas the hindlimb grows most rapidly during middle ontogeny, suggests a postural shift from quadrupedality to bipedality during the growth of *P. lujiatunensis*. In early ontogeny the forelimb may have been growing rapidly, in order to maintain its proportional length and role in locomotion, whereas in middle ontogeny the simultaneous slowing of forelimb growth and acceleration of hindlimb growth may have caused the hindlimb to increase in relative length and assume primary responsibility for locomotion. However, the nature of the linkage between vascular canal orientation and the rate of length increase of a given bone requires further investigation, and the hypothesis that a postural shift took place in the growth of *P. lujiatunensis* requires further testing on the basis of measured changes in limb proportions (see below).

I conclude that the histological evidence for a postural shift presented in this study for *P. lujiatunensis* is corroborated by histological evidence (Erickson and Tumanova, 2000) in another species of *Psittacosaurus*, *P. mongoliensis*. In both cases, histology shows a differential change in bone apposition at midshaft, with the hindlimb bones speeding up growth relative to the forelimb bones. The specific changes in histology differ in both species of *Psittacosaurus*, and this shift happened at a larger body size in *P. mongoliensis* than in *P. lujiatunensis*, consistent with the presumably larger final body size of the former.

4.3.2 Limb proportions and limb posture through ontogeny in *P. lujiatunensis*

Psittacosaurus has been generally regarded as a habitual or obligate biped (Chinnery, 2004; Chinnery and Horner, 2007; Osborn, 1924; Senter, 2007; Sereno, 1990, 1997b), although the structure of the manus (Sereno, 1990, 1997b) and a few other skeletal features (Maryanska and Osmólska, 1985) have been interpreted as indicating at least some quadrupedal capability. A recent analysis of the distribution of osteological correlates of quadrupedality among ornithischians strongly favoured the view that *Psittacosaurus* was mainly bipedal (Maidment and Barrett, in press). Ornithischian quadrupeds typically possess a large anterolateral process on the ulna, hoof-like manual unguals, an everted dorsal edge of the ilium, a reduced fourth trochanter, and a femur whose length exceeds that of the tibia. In *P. lujiatunensis* specimens of any age the proximal end of the ulna bears only a small, laterally directed bulge, the dorsal edge of the ilium is narrow and non-everted, the fourth trochanter is large and pendant when preserved intact, and the tibia is slightly longer than the femur. Few well-preserved manual unguals are present in mysample. The available examples are shorter relative to their width than the pedal unguals, but are clearly pointed rather than hoof-like. This suite of characters, which is shared with other very basal ceratopsians (Maidment and Barrett, in press), strongly suggests that *P. lujiatensis* was bipedal. However, this interpretation may only apply to adults. Ontogenetic changes in the various indicators of quadrupedality have not been investigated (Maidment and Barrett, in press), and it is uncertain how the features in question would be affected by an ontogenetic postural shift of the kind inferred to have taken place in some dinosaurs.

The forelimb-to-hindlimb ratio has traditionally used as a postural indicator in dinosaurs (Galton, 1970), with high ratios being considered indicative of quadrupedality. However, the utility of this metric in distinguishing quadrupeds from bipeds may be limited (Maidment and Barrett, in press). The ratio in subadult to adult *P. lujiatunensis* as determined in this study (0.59 – 0.66) corresponds to the lower part of that reported by Maidment and Barrett (Maidment and Barrett, in press) for eurypodan thyreophorans, even though other osteological indicators point clearly to bipedality for *Psittacosaurus* and quadrupedality for eurypodans. Similarly, the ancestral value of 0.67 reconstructed by Maidment and Barrett (Maidment and Barrett, in press) for the unambiguously quadrupedal ceratopsids falls only just outside the range for sub-adult to adult *P. lujiatunensis*. There appears to be a range of values consistent with either bipedality or quadrupedality.

However, the forelimb-to-hindlimb ratio is extremely high (averaging 0.84) in hatchlings of *P. lujiatunensis*, far exceeding values typical of eurypodans, ceratopsids and other quadrupedal dinosaurs (Maidment and Barrett, in press). The extreme values seen in hatchlings strongly suggest that they were essentially quadrupeds. This points to an ontogenetic shift along the continuum from quadrupedality to bipedality in the ontogeny of *P. lujiatunensis*, although the shift was not necessarily between obligate versions of the former and latter conditions. It is possible, for example, that hatchlings were primarily quadrupedal but resorted to bipedality at high speeds, whereas adults were quadrupedal only when moving very slowly. However, the proportionally long forelimbs of hatchlings, combined with the skeletal evidence for bipedality in adults, clearly implies that at least a limited postural shift took place. I envision the body of *P. lujiatunensis* as fundamentally suited to bipedality (Maidment and Barrett, in press). Hatchlings, however, were equipped with long forelimbs that could have been

placed on the substrate when necessary to provide needed stability, particularly during slow locomotion. As an individual matured, its forelimb would have grown proportionally shorter and its balance would presumably have improved, so that the forelimb would have contacted the substrate less often.

Histology contributes to understanding the ontogeny of posture in *P. lujiatunensis* in that counting LAGs makes it possible to relate changes in forelimb-to-hindlimb ratio to age in years, demonstrating that very high values were confined to specimens with less than one LAG. One-year-olds may have already been significantly less quadrupedal than hatchlings, and any subsequent changes were gradual.

Patterns of growth inferred from measurements of long bones can also be compared to patterns of bone deposition as inferred from histology. The two lines of evidence agree, and reinforce each other, to the extent that both suggest a shift from quadrupedality to bipedality based on an increasing length discrepancy between the hindlimb and the forelimb over the course of ontogeny. However, histology also suggests that the shift occurred sometime after completion of the third year of growth, when forelimb growth accelerated and hindlimb growth was retarded, while measurements of long bones imply that the shift was at least initiated earlier based on rapid decrease in the forelimb-to-hindlimb ratio during early ontogeny. Furthermore, long bone measurements do not appear to confirm the histological evidence for particularly rapid growth of the forelimb bones during early ontogeny, and particularly rapid growth of the hindlimb bones during middle ontogeny. It is likely that these discrepancies between histological evidence and limb bone measurements regarding growth in *P. lujiatunensis* are at least partly the result of inadequate sample size, and of random variation in the limb proportions of the individuals in the data set.

Although measurements of limb bones provide strong evidence for a shift towards greater bipedality, these data may be spread too thinly across ontogeny to reliably provide precise information about when and how the shift took place. However, the discrepancies between histological and measurement-based inferences about growth also suggest that the relationship between vascular canal orientation and rate of increase in actual bone dimensions requires further investigation. This relationship may be a particularly fruitful area for future histological research.

4.3.3 Postural shifts in other dinosaurs

The negative forelimb allometry that evidently characterized the ontogeny of *P. lujiatunensis* is comparable to that previously reported in the sauropodomorph dinosaur *Massospondylus*, which is inferred based on patterns of limb bone allometry to have been quadrupedal as a hatchling but to have shifted to a bipedal posture later in ontogeny (Reisz et al., 2010; Reisz et al., 2005). Even hatchlings of at least some therizinosaurian theropods may have been preferentially quadrupedal, given the existence of embryonic specimens whose forelimbs are nearly equal in length to their hindlimbs (Kundrat et al., 2008), although in the absence of actual preserved hatchlings this inference must be considered uncertain. An ontogenetic shift from quadrupedality to bipedality has also been inferred in the ornithopod *Dryosaurus*, based on changes in the cross-sectional geometry of the femur during growth (Heinrich et al., 1993). By contrast, the ornithopods *Maiasaura* and *Iguanodon* are inferred to have undergone a postural shift from juvenile bipedality to adult quadrupedality (Dilkes, 2001; Norman, 1980).

The findings of the present study add to a growing body of evidence suggesting that ontogenetic quadrupedal-to-bipedal postural shifts were widespread in dinosaurs. Such shifts have now been inferred to have taken place in some members of at least two of the three major dinosaurian clades, namely Sauropodomorpha and Ornithischia. There is even a possible example of such a shift within the third clade, Theropoda, based on the elongate forelimbs that have been reported in therizinosaurian embryos (Kundrat et al., 2008). However, the humerus measures 55-65% of the length of the femur in some theropod embryos, including oviraptorid (Weishampel et al., 2008) and troodontid (Varricchio et al., 2002) specimens, in striking contrast to the near-equality in length between the humerus and femur seen in the therizinosaurians (Kundrat et al., 2008). It is clear that hatchlings were bipedal in some theropods, even if they were quadrupedal in at least some therizinosaurians.

Selection acting on juveniles must have favoured bipedal hatchlings in some theropods and ornithopods, but quadrupedal hatchlings in other theropods, some ornithischians, and at least some sauropodomorphs. The possibility that basal members of all three major dinosaurian clades retained a quadrupedal hatchling stage is intriguing and cannot presently be excluded, but awaits confirmation or refutation based on future discoveries. Similarly, the quadrupedal-to-bipedal shifts that occur in at least some taxa may recapitulate the evolutionary transition from quadrupedal basal archosaurs to bipedal avemetatarsalians that took place during the Early and Middle Triassic (Brusatte et al., 2011; Sereno, 1991), but this scenario will remain speculative until much more information is available regarding the ontogeny of the early avemetatarsalian bipeds themselves.

My study highlights the potential benefits of considering histology alongside limb proportions and qualitative morphological features in studying the ontogeny of

posture and locomotion in a fossil tetrapod. Counting LAGs makes it possible to roughly determine the age of each individual sampled, which provides a basis for determining the timing of changes in both limb bone measurements and patterns of vascular canal orientation. Measurements of limb bones for individuals of known ages can be used to build up a direct but discontinuous record of growth, defined as increase in bone dimensions, whereas the complementary record provided by vascular canal orientation and other histological features is indirect but continuous. Quantitative analysis of the link between histological indicators of bone growth and changes in the actual dimensions of long bones remains as an intriguing avenue for future research, and one that may eventually make it possible to use histology as a basis for more precise inferences about growth patterns and postural shifts.

Chapter 5 Juvenile-only clusters and behaviour of the Early Cretaceous dinosaur *Psittacosaurus*

Author Contribution: This chapter has been accepted for publication in *Acta Palaeontology Polonica:*

Zhao, Q., Benton, M. J., Xu, X., and Sander, M. P. Histological evidence for timing of posture shift during early growth of ceratopsian dinosaurs

This study built upon the initial PhD project outline as written by M. J. Benton. Discussion with M. J. Benton, X. Xu, and M. P. Sander, who also reviewed and edited the manuscript during preparation, Q. Zhao is the lead and corresponding author of this paper and has contributed all of the work in analysing the data and preparing the manuscript.

5.1 Introduction

Social behaviour is a very interesting topic palaeontology, but also hard to be proved in fossils. Fortunately, in recently years, there are lots of wonderful fossils were found in Northeast of China. Some of these fossils preserved very good information on social behaviour. Bone histology can proved more details to support the social behaviour research. A previously described specimen, which consists of an 'adult' *Psittacosaurus* with 34 fully articulated juveniles, will be reanalyzed the reality in this chapter. A remarkable juvenile-only cluster of *Psittacosaurus* which shows evidence of different ages will also be reanalyzed by bone histology research. In this chapter, we will make a review of juvenile-only behaviour in dinosaurs.

5.1 Results

5.1.1 Age determination from bone histology

There is extensive evidence that dinosaurs grew episodically. Although they had high metabolic rates, and so laid down primarily fibro-lamellar bone, indicating high growth rate (Amprino, 1947), they all seem to show one episode each year when growth rates slowed and a dense layer is deposited in the bone, termed a line of arrested growth (LAG) (Chinsamy-Turan, 2005). Such LAGs could represent numerous episodes of slow growth, mainly resulting from food shortage or low precipitation events rather than sudden cooling (Kohler et al., 2012), each year, but there are no reports of only one LAG formed every two years, which supports the deduction that LAGs in fossil vertebrates are more than likely annual (Chinsamy-Turan, 2005). Seasonality appears to be the main factor for the cyclical growth pattern

in bones of reptiles (Peabody, 1961). However, the occurrence of LAGs in bones of extant reptiles and amphibians living in non-seasonal environments (Chinsamy et al., 1995) indicates that the cyclical variations in osteogenesis and growth are the result of an inherent (genetic) rhythm that becomes synchronized with and reinforced by seasonal cycles (Castanet et al., 1993).

If LAGs represent annual markers in the bone (Kohler et al., 2012), then individual dinosaur skeletons can be aged, and growth curves can be compiled. Such growth curves for a wide range of dinosaurs (Erickson et al., 2001), such as *Psittacosaurus mongoliensis*, show classic sigmoid growth curves, with an early phase of slow growth in years 1-2, a burst of rapid growth in years 5-10, and a slowing of growth in years 10-15. As growth slows, comparison with growth curves for living vertebrates suggest that this marks the attainment of sexual maturity and adult size. Studies of series of juvenile to adult skeletons and bone histological analysis of *Psittacosaurus mongoliensis* (Erickson and Tumanova, 2000) and *P. lujiatunensis* (Erickson et al., 2009) show that sexual maturity began no later than the tenth year of life.

5.1.2 Evidence from bone histology for a mixed-age juvenile group in IVPP V14341

The largest individual in this cluster is IVPP V14341.1 (Fig. 1.1). Thin sections show three LAGs in the humerus, femur and fibula, but just two LAGs in the tibia. Medullary cavity expansion may have obliterated the first-year LAG in this tibia. I studied four tibial thin sections from different individuals of the same cluster. There are just two LAGs in each thin section. Using a camera lucida, I drew each section

including the LAGs under the microscope and then superimposed the drawings. I found the medullary cavity of the tibia of IVPP V14341.1 to be much larger than in the others, and its size overlaps with the first-year LAG in the other tibiae (IVPP V14341.2-5).

To test this, I sampled five fibulae and one radius thin sections from different individuals of IVPP V14341. The mid-diaphyseal transverse section of the fibulae showed three LAGs in IVPP V14341.1 (Fig. 4.1*a*), and two LAGs in the other four individuals (Fig. 4.1*c-e*). The thin sections of the radius from IVPP V14341.6 also just showed two LAGs. This is consistent with the LAG count for the tibiae of the smaller specimens and the resorption of one LAG in the tibia of the larger specimen.

All the thin sections from this cluster thus indicate that the offspring came from two different clutches, separated by about one year.

5.1.3 Description of the thin sections

The cortex of the fibular diaphysis of IVPP V14341 is fibro-lamellar bone with predominantly longitudinal vascular canals and very few simple reticular vascular canals. The degree of vascularization is high, and only primary osteons can be observed in the thin sections. The degree of vascularization at age 2 is relatively higher than it is at age 3. No external fundamental system of closely packed peripheral growth lines was found in these thin sections.

The presence of fibro-lamellar bone tissue shows a very fast grow rate. This kind of bone tissue is usually found in juvenile or sub-adult individuals (Chinsamy, 1995). The absence of secondary osteons suggests that the observed tissue had not been remodeled (Xu et al., 2012). All this evidence suggests these individuals are juveniles.

5.1.4 Statistical analysis of the correlation between skull length and age in *Psittacosaurus lujiatunensis*

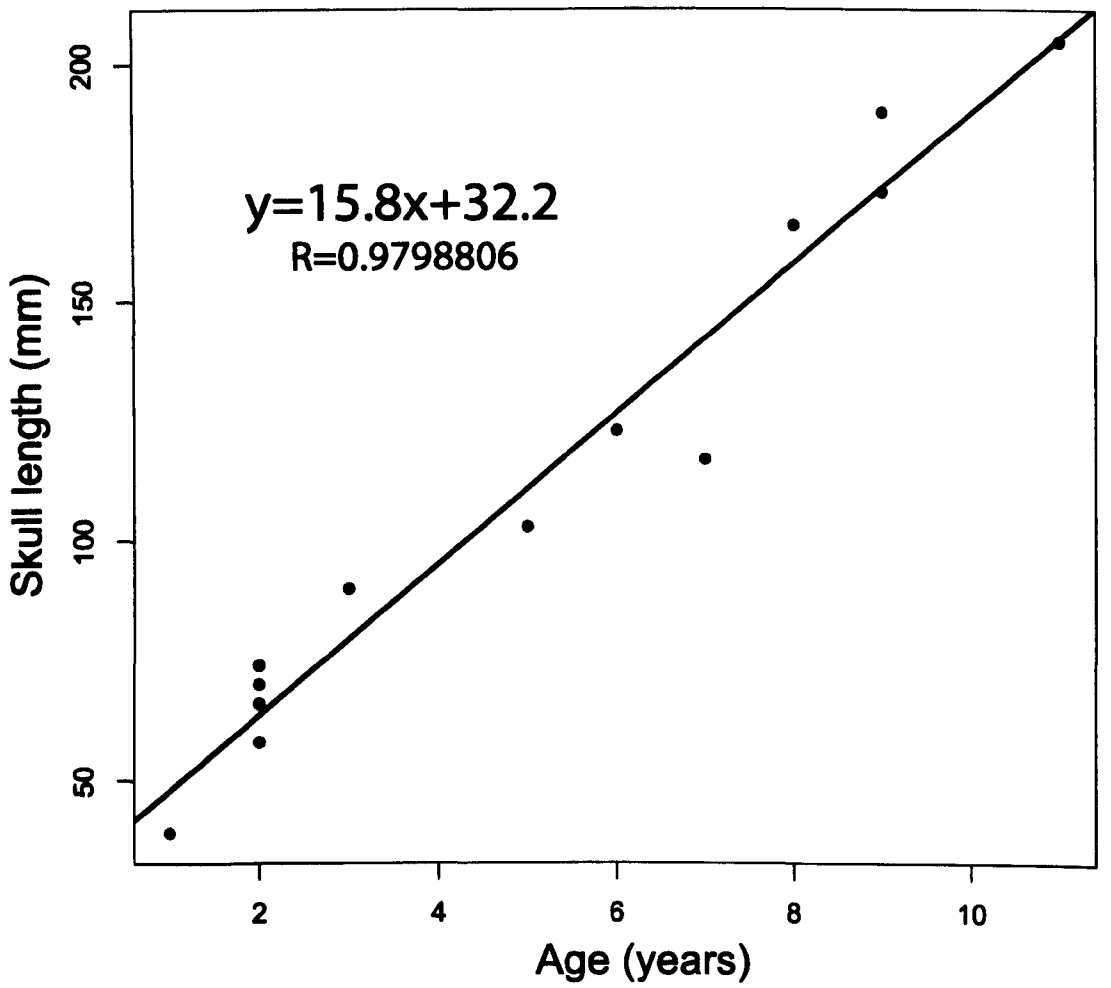

Figure 5.1 Isometric growth in *Psittacosaurus lujiatunensis*.

Skull length/ femur length (y-axis) increases linearly with estimated age, in years (x-axis). The plot is based on measurements of 13 specimens (see 3.3.7).

Specimen number	Age (yrs)	Skull length (mm)	Femur length
IVPP V16902.6	1	39	34
IVPP V14341.1	3	90	73
IVPP V14341.2	2	58	53
IVPP V14341.3	2	66	55
IVPP V14341.4	2	70	61
IVPP V14341.5	2	74	65
IVPP V14748	5	103	107
IVPP V14749	6	123	113
IVPP V12716	9	173	160
ZMN M8137	9	190	189
ZMN M8138	11	205	202
PKUVP V1053	7	117	149
PKUVP V1054	8	166	164

Table 5.1 Measurments of skull and femur length of *Psittacosaurus lujiatunensis* in different ages.

These data are used in Figure 5.1. The data were tested for normality by a Q-Q plot (below) showing the age, skull length and femur length. The correlation coefficient between age and skull length is 0.9798806; Pearson's product-moment

correlation, t=16.2833. df=11, p-value=4.789e-09. These mean there is a strong positive linear relationship. Further, there is strong evidence against the null hypothesis of zero correlation in the population (p = 4.789e-09). The 95 percent confidence interval (0.9321781, 0.9941335) is also very narrow.

The coefficient analysis between the skull length and age in R:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	32.153	5.900	5.45	0.000201 ***
Age	15.761	0.968	16.28	4.79e-09 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*'

Residual standard error: 11.36 on 11 degrees of freedom

Multiple R-squared: 0.9602, adjusted R-squared: 0.9565

F-statistic: 265.1 on 1 and 11 DF, p-value: 4.789e-09

5.1.5 Mixed-age juvenile groups of *Psittacosaurus*

In the specimen, IVPP V14341, a cluster of six juvenile skeletons, I show that these vary in age – one is three years old, the others two, based on their bone histology. I have to demonstrate first that this is a natural cluster, and not the result of sedimentary accumulation, and then that I have a reliable method of age determination. These topics are discussed in turn. It should be noted that I do not claim that *Psittacosaurus* juveniles always occur in juvenile-only clusters. Other specimens from Lujiatun consist of individuals of mixed ages, and others were single

specimens representing various developmental stages, but juvenile-only clusters are common.

5.1.6 Previous report of parental care in *Psittacosaurus*

Some of the most widely discussed examples of clusters of juveniles are those of the Early Cretaceous basal ceratopsian *Psittacosaurus*. A remarkable cluster of 34 juveniles was reported from the Lujiatun site in Liaoning Province, China, apparently associated with the skull of an adult (Meng et al., 2004).

Meng et al. (2004) reported 34 fully articulated *Psittacosaurus* juveniles in the parental care of an adult. As Varricchio et al. (2007) mentioned, this parental care clutch remains taphonomically ambiguous, and I now suggest unequivocally that the subadult skull has been added. In any case, it is highly unlikely that a female could produce a clutch of such size (Isles, 2009). Studies of series of juvenile to adult skeletons and bone histological analysis of *Psittacosaurus mongoliensis* (Erickson and Tumanova, 2000) and *P. lujiatunensis* (Erickson et al., 2009) show that sexual maturity began no later than the tenth year of life. The 34 juveniles have femora 30-34 mm long, and so these individuals might have been 1 year old, based on comparisons with myhistologically aged specimens in IVPP V14341 (femora 53-65 mm long in 2-year-olds; see below). My close inspection of this cluster of 34 juveniles (DNHM D2156) shows that the 'adult' skull has been added, and so was not part of the original specimen; there is no sedimentary connection to the main slab below, and the skull rests loosely on top of that slab, and is not in any way part of the sedimentary layer in which the juveniles all occur, intertwined with each other. The evidence is that the 'adult' skeleton just contains a few postcranial bones without any articulation,

and the skull position is much higher than the juvenile bone-bed plane. The juveniles all seem to belong together because they are preserved at one level in the rock, and their limbs and tails overlap each other in complex ways.

Even if the larger skull were truly associated with the cluster of juveniles in this specimen, it could not be asserted that this was the 'mother' of those juveniles, because the large skull is subadult, not adult. It is unlikely that a female could produce a clutch of such size, based on wider comparison of female sizes and clutch sizes across archosaurs (Isles, 2009). Studies of series of juvenile to adult skeletons and bone histological analysis of *Psittacosaurus mongoliensis* (Erickson and Tumanova, 2000) and *P. lujiatunensis* (Erickson et al., 2009) show that sexual maturity began no later than the tenth year of life. The 34 juveniles have femora 30-34 mm long, and so these individuals might have been 1 year old, based on comparisons with myhistologically aged specimens in IVPP V14341 (femora 53-65 mm long in 2-year-olds; see below). Further, the dimensions of the 'adult' skull (about 125 mm) suggest it came from a 6-year old animal, still too young to breed (the breeding age for *Psittacosaurus* is about 10 years old (Erickson et al., 2009)). The isometric growth line (Fig. 5.1) *of Psittacosaurus lujiatunensis* shows the relationship between skull length and age

The Dalian specimen then does not show a mother and her young, as first suggested (Meng et al., 2004), but a subadult skull artificially associated with a genuine cluster of 34 yearlings. Such a large juvenile-only cluster is in itself important evidence about dinosaurian behaviour, and is in line with other evidence of juvenile-only clusters.

5.1.7 Biological association, not sedimentary accumulation.

As noted in Zhao et al. (2007), the six skeletons come from the Lujiatun locality in Liaoning. The geology of the site shows that the fossils are preserved within pyroclastic flow deposits (Eberth et al., 2010; Jiang and Sha, 2007; Jiang et al., 2012; Jiang et al., 2011; Zhao et al., 2007). By examining the matrix though petrology, petrography and X-ray diffraction, the sediment in which the skeletons occur represents a lahar (volcanic mudflow), indicating that the six individuals present were entombed simultaneously during a catastrophic mass mortality event. A great deal of evidence to supports this hypothesis. For example, the matrix exhibits a wholly massive texture with no evidence of grading or sorting. Iron oxide rinds or halos are absent around grains and there is no evidence of invertebrate bioturbation or plant roots. Furthermore, the massive texture, matrix-supported grains and pebbles, very poor size sorting, mixture of fresh and weathered grains, and absence of evidence for bioturbation all indicate that the host matrix was deposited by massive flows that were very likely cohesive and possibly of high density. This interpretation clearly excludes an origin from suspension or turbulent flows (hydraulic or aeolian) and suggests, instead, that the matrix containing the *Psittacosaurus* skeletons was deposited as a lahar, either during the eruptive phase of a nearby volcanic centre, or during a non-eruptive debris flow event that reworked previously deposited volcanic material (Fisher and Schmincke, 1984).

A lahar interpretation is fully compatible with the high-quality in situ preservation of the psittacosaur specimens. As demonstrated by Fisher and Schmincke (1984), it is common for lahars to bury sedimentary surfaces and organic remains across low-gradient slopes (< 10 degrees) without erosion, transport or other modification, even when travelling over distances of up to 80 km. Consequently,

although little is known about the precise palaeogeography of the Lujiatun psittacosaur locality, Zhao et al. (2007) reasonably conclude that the site was located a significant distance downslope from a volcanic centre where the gradient was 10 degrees or less.

This is a most unusual mode of preservation for dinosaur fossils. In most cases (Dodson et al., 1980; Norman, 1980, 1987; Roach and Brinkman, 2007), dinosaur bones are preserved in ancient river sediments, sometimes in channel lags or channel bars, in which case numerous carcasses may have accumulated over a long time span, extending to months or even years. The carcasses might all be equally well articulated, and in apparently identical physical condition of preservation, but nonetheless they might have accumulated through a series of annual flood events, and so represent a time-averaged assemblage. In such a case, it could not be assumed that the association says anything about the original life habitat or the original putative gregarious behavior of the dinosaurs.

5.2 Discussion

Juvenile-only clusters in *Psittacosaurus*, ranging from five to 34 individuals, and with evidence for a variety of ages in at least one specimen (IVPP V14341) suggests some unique juvenile-only behaviour. Perhaps *Psittacosaurus* juveniles congregated for protection, for a specialized diet, or for helping at the nest. Today, juvenile-only flocks or herds of birds and mammals may exist for protection (Pelletier and Festa-Bianchet, 2004) and this may have been the same for dinosaurs after they had hatched and become self-sufficient (Myers and Fiorillo, 2009). Erickson suggested that *Psittacosaurus lujiatunensis* appears to have reached threshold sizes

somewhere between 3 and 4 years old, as these animals were entering the transition to the exponential stage of growth when they would have explosively increased in body mass (Erickson et al., 2009). It is considered that under 4 years old, young *Psittacosaurus* still need to gather together to protect each other. Indeed, direct fossil evidence (Hu et al., 2005) shows that the triconodont mammal *Repenomamus* ate juvenile *Psittacosaurus* on occasion, and small herds of juveniles might have existed for their own protection from predators.

In addition, there is some circumstantial evidence for a change in diet during ontogeny of *Psittacosaurus*: the presence of numerous large gastroliths in adult *Psittacosaurus* suggests a high-fibre, nut-eating diet (Sereno, 2010). Gastroliths have not been found in any juvenile psittacosaurs, and so they may have eaten a less fibrous diet. Different diets between juveniles and adults would indicate different locations and modes of foraging for food, and the likelihood that juveniles and adults might be found in age-specific clusters in different locations. Such a dietary switch has been hypothesized in many dinosaur groups (Codron et al., 2012), and in each case might have been associated with a major change of behaviour.

The third suggestion, that *Psittacosaurus* juveniles may have acted as 'helpers at the nest', is even more circumstantial. Among modern birds, juveniles in many clades stay around their parents and their nests and may help the parents bring up subsequent broods; this is interpreted as a way in which the non-breeding juveniles may increase their genetic fitness until they are of breeding age themselves(Hamilton, 1963; Hatchwell, 2009; Skutch, 1961). It is also a reason that juveniles from different year classes, assuming an annual breeding regime, might be found associating together, and would imply that all juveniles, of whatever age, might have been siblings.

Chapter 6 Phylogeny, diversity and disparity of Ceratopsia

Author Contributions: This chapter has not previously been published. All material herein is the work of Q. Zhao

6.1 Phylogeny analysis and results

6.1.1 Introductions of previous phylogeny analysis

Ceratopsia consists of Psittacosauridae and Neoceratopsia, the later formed by numerus basal taxa and Ceratopsidae (You and Dodson, 2004). In recent years, serval new basal ceratopsia were found, such as Yinlong (Xu et al., 2006), *Xuanhansaurus* and *Liaoceratops yanzigouensis* (Xu et al., 2002). The phylogentic reasearch in Ceratopsia is mainly foucsed on ceratopsidae (Dodson et al., 2004; Farke, 2011; Forster, 1990a; Ryan, 2007; Sampson et al., 2010; Wu et al., 2007) or basal ceratopsia (Averianov et al., 2006; Chinnery and Horner, 2007; Lee et al., 2010; Makovicky and Norell, 2006; Sereno, 2000; Xu et al., 2006; You and Dodson, 2004). These phylogenetic analyses also have some conflicts. For example, Makovicky and Norell (2006) place *Yamaceratops* between *Archaeoceratops* and *Liaoceratops*, but Chinnery and Horner (2007) considered *Yamaceratops* and *Leptoceratops* are sister groups.

The main reason for these conflicts is the uncompleted data matrix. So in my study, I try to make a super matrix to including all the ceratopsians we known.

6.1.2 Analysis

The super matrix including 318 characters scored for 62 in-group taxa and 1 out-group taxon. Most of the data are collected from other literatures (Averianov et al., 2006; Chinnery and Horner, 2007; Dodson et al., 2004; Farke, 2011; Forster, 1990a; Lee et al., 2010; Makovicky and Norell, 2006; Ryan, 2007; Sampson et al., 2010; Sereno, 2000; Wu et al., 2007; Xu et al., 2006; You and Dodson, 2004). I

recoded some Chinese ceratopsians, such as *Yinlong, Psittacosaurus lujiatunesnsis, Psittacosaurus neimongoliensis, Liaoceratops yanzigouensis, Archaeoceratops oshimai* and *Magnirostris dodsoni.*

Because some taxa just preserved very few elements, these makes a lot of questions marks in the matrix. According to the reduced consensus method of Wilkinson (2001), I eliminated the problematic taxa: *Koreaceratops hwaseongensis, Auroraceratops rugosus, Zhuchengceratops inexpectus, Ojoceratops fowleri, Eotriceratops xerinsularis, Sinoceratops zhuchengensis, Rubeosaurus ovatus,* and *Tatankaceratops sacrisonorum.*

Heuristic search found 480 MPTs: L=671 steps, CI = 0.604, RI = 0.848, RC = 0.512, HI = 0.396. (Fig. 6.1)

6.1.3 The topology of the basal ceratopsian phylogeny

Chaoyangsaurus youngi (Zhao et al., 1999) is an enigmatic basal taxon based on a holotype that was found several decades ago. According to cladistic analysis, *Chaoyangsaurus youngi* is considered to be the most basal neoceratopsian. But by my analysis, *Chaoyangsaurus youngi* was posited to lie outside of the neoceratopsian-psittacosaurid clade. The same result has also been found by Makovicky (2001) and Xu et al. (2002).

Psittacosaurus is a typical monogeneric clade. In my analysis (Fig. 6.1), *Psittacosaurus lujiatunensis* was fully recorded, and *Psittacosaurus lujiatunensis* is clearly the sister taxon of *Psittacosaurus major.* This phylogenetic hypothesis supports Sereno (2010), but differs from You et al. (2008). *Psittacosaurus gobiensis* was included in the cladistic analysis for the first time, and becomes the sister group

of a clade of *Psittacosaurus sinensis* and *Psittacosaurus neimongoliensis*. The position of *Psittacosaurus meileyingensis*, *Psittacosaurus mongoliensis*, and *Psittacosaurus mongoliensis* is uncertain in my analysis.

6.1.4 The topology of basal Neoceratopsia

Neoceratopsia, the stem-based clade defined as all ceratopsians more closely related to *Triceratops* than to *Psittacosaurus*, shares the following characters: an enlarged head relative to the body; a keeled rostral end of the rostral bone; a short jugal process of the postorbital; a much reduced quadratojugal; the basioccipital excluded from the formation of the foramen magnum; the coronoid process covering the caudal tooth row in lateral view; a primary ridge on the maxillary teeth; a caudal process on the coracoid; the development of the humeral head; and a gently decurved ischium (You and Dodson, 2004).

Different from all the other cladistic analyses, I found that *Yinlong downsi* is the most basal neoceratopsian instead of *Chaoyangsaurus youngi* (Fig. 6.1). *Yinlong downsi* shows some characters that are similar to the basal neoceratopsians, such as rostral ventral (buccal) process is present; external naris shape is elliptical and position is high separated by a flat area.

Ajkaceratops kozmai, the first undoubted ceratopsian found in Europe, was also for the first time included in a cladistic analysis. The analysis shows it in the group of *Protoceratops*, and is closest to *Bagaceratops rozhdestvenskyi*. Osi et al. (2010) considered *Ajkaceratops* maybe to be a dwarfed taxon, and still required further discoveries to determine this. If *Ajkaceratops* is a dwarfed taxon, I suppose it is a dwarfed taxon of *Protoceratops*.

The relationship of *Leptoceratops, Udanoceratops*, and *Prenoceratops* is uncertain in Makovicky and Norell (2006). But in my analysis, *Leptoceratops* and *Udanoceratops* are sister groups, and *Prenoceratops* lies just outside the clade of *Leptoceratops* and *Udanoceratops*.

Bainoceratops efremovi from South Mongolia was not included in any cladistic analysis before. In my analysis, it is the sister taxon to the clade of *Leptoceratops, Udanoceratops*, and *Prenoceratops*.

Montanoceratops was considered to be a sister taxon to *Prenoceratops* in previous research (Chinnery and Horner). But based on my analysis, *Montanoceratops* lies outside the clade of *Bainocertaops*, *Leptoceratops, Udanoceratops*, and *Prenoceratops*.

The hypothesis that *Zuniceratops* and *Turanoceratops* are successive out groups to the traditional ceratopsid crown group of Centrosarinae and Chasmosaurinae was first raised by Wolfe and Kirkland (1998), but with no cladistic analysis. They defined a new clade Ceratopsomorpha to include all ceratopsian taxa bearing brow horns in their ancestry. My analysis supports this hypothesis based on cladistic analysis.

6.1.5 The topology of Ceratopsidae

The monogeneric clade Ceratopsidae consists of two subclades, Centrosaurinae and Chasmosaurinae. Centrosaurinae is defined as Ceratopsidae closer to *Centrosaurus* than to *Triceratops*. For the phylogeny of Centrosaurinae, the internal topology of *Einiosaurus procurvicornis*, *Achelousaurus horneri*, *Pachyrhinosaurus canadensis*, *Pachyrhinosaurus lakustai*, *Styracosaurus albertensis*,

Centrosaurus apertus is uncertain in the strict consensus tree, but the positions of their outgroup taxa (*Avaceratops lammersi, Albertaceratops nesmoi,* and *Diabioceratops eatoni*) are much clear (Fig. 6.1). While in the strict consensus tree of Farke et al. (2011), there is a very clear internal topology of *Einiosaurus procurvicornis, Achelousaurus horneri, Pachyrhinosaurus canadensis, Pachyrhinosaurus lakustai, Styracosaurus albertensis, Centrosaurus apertus,* but the position of *Avaceratops lammersiand Albertaceratops nesmoi* is uncertain.

Chasmosaurinae is defined as all members of Ceratopsidae closer to *Triceratops* than to *Centrosaurus*. The clade of Chasmosaurinae also consists of two subclades in the strict consensus tree (Fig. 6.1). One clade is all the members of Chasmosaurinae closer to *Chasmosaurus* than to *Triceratops.* This clade is united by five unambiguous synapomorhphies: bony flange on posterior margin of narial strut, forked distal end of posteroventral process on premaxilla, nasal ornamentation position centred posterior or posterodorsal to internal naris, parietal median bar narrow and straplike, and parietal concave median embayment on caudal margin. These unambiguous synapomorphies are not the same as in Dodson et al. (2004). These authors noticed three unambiguous synapomorphies: bony flange along the caudal margin of the narial strut, forked distal end of the premaxillary caudoventral process, and large parietal fenestrae (45% or more total parietal length). In this clade, the position of the taxa is much clearer compared to other clades, just a little bit weaker in the higher-level relationships.

Another clade is all the members of Chamosaurinae closer to *Triceratops* than to *Chasmosaurus*. In the phylogenetic strict consensus tress (Fig. 6.1), *Arrhinoceratops* is a sister group to *Anchiceratops. Nedoceratops, Torosaurus* and *Triceratops* comprise a clade, but their internal topology is uncertain.

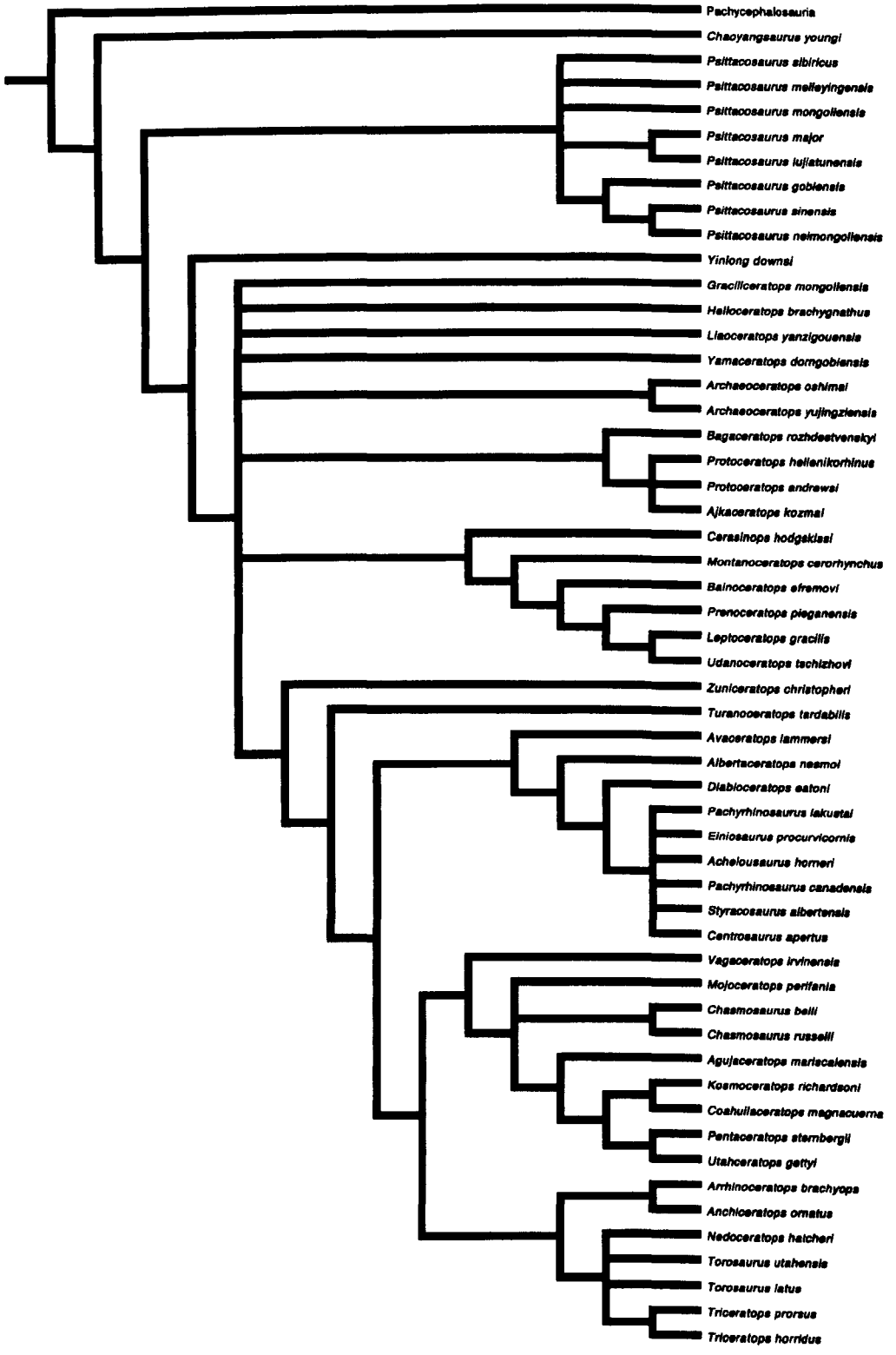

Figure 6.1 Safe Taxonomic Reduction strict consensus tree.

Based on safe taxonomic reduction (Wilkinson, 1995, 2003), eight taxa were removed to get a high-resolution strict consensus. Safe taxonomic reduction was implemented using the programs TAXEQ3 (Wilkinson, 2001b) and REDCON 3.0 Wilkinson (2001a).

6.2 Result of diversity analysis

The phylogram with ghost lineage (Figure 6.2) is used to calculate the phylogenetic diversity estimates (PDE), which contains 49 genera and 62 species.

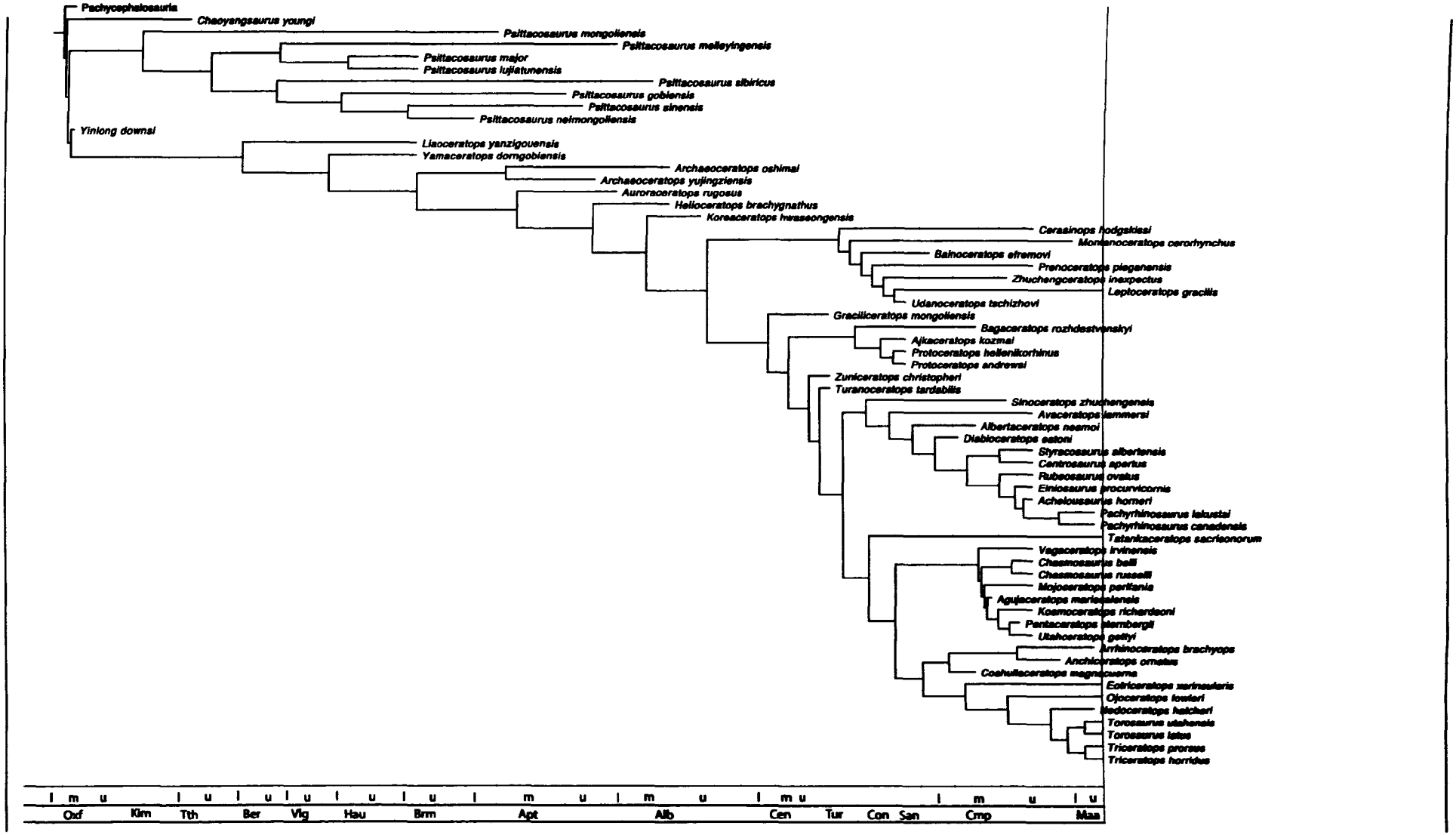
Pachycephalosauria
Chaoyangsaurus youngi
Psittacosaurus mongoliensis
Psittacosaurus meileyingensis
Psittacosaurus major
Psittacosaurus lujiatunensis
Psittacosaurus sibiricus
Psittacosaurus gobiensis
Psittacosaurus sinensis
Psittacosaurus neimongoliensis
Yinlong downsi
Liaoceratops yanzigouensis
Yamaceratops dorngobiensis
Archaeoceratops oshimai
Archaeoceratops yujingziensis
Auroraceratops rugosus
Helioceratops brachygnathus
Koreaceratops hwaseongensis
Cerasinops hodgskissi
Montanoceratops cerorhynchus
Bainoceratops efremovi
Prenoceratops pieganensis
Zhuchengceratops inexpectus
Leptoceratops gracilis
Udanoceratops tschizhovi
Gracilicerátops mongoliensis
Bagaceratops rozhdestvenskyi
Ajkaceratops kozmai
Protoceratops hellenikorhinus
Protoceratops andrewsi
Zuniceratops christopheri
Turanoceratops tardabilis
Sinoceratops zhuchengensis
Avaceratops lammersi
Albertaceratops nesmoi
Diabloceratops eatoni
Styracosaurus albertensis
Centrosaurus apertus
Rubeosaurus ovatus
Einiosaurus procurvicornis
Achelousaurus horneri
Pachyrhinosaurus lakustai
Pachyrhinosaurus canadensis
Tatankaceratops sacrisonorum
Vagaceratops irvinensis
Chasmosaurus belli
Chasmosaurus russelli
Mojoceratops perifania
Agujaceratops mariscalensis
Kosmoceratops richardsoni
Pentaceratops sternbergi
Utahceratops gettyi
Arrhinoceratops brachyops
Anchiceratops ornatus
Coahuilaceratops magnacuerna
Eotriceratops xerinsularis
Ojoceratops fowleri
Medoceratops hatcheri
Torosaurus utahensis
Torosaurus latus
Triceratops prorsus
Triceratops horridus
l m u l u l u l u l u l u l m u l m u l m u l m u l u
Oxf Kim Tth Ber Vlg Hau Brm Apt Alb Cen Tur Con San Cmp Maa

Figure 6.2 Phylogram with ghost lineage based on the strict consensus tree and lasted published cladograms (Farke et al., 2011; Makovicky and Norell, 2006; Sampson et al., 2010; Sereno, 2010)

According to the analysis, I found the ceratopsian diversity (Fig 6.3) is low from the Early Jurassic to the early Early Cretaceous (from Berriasian to Hauterivian). Ceratopsian diversity shows a marked increase during the later Early Cretaceous (from Barremian to Albian). However, the diversity of ceratopsians dropped dramatically during early Late Cretaceous (from Cenomanian to Turonian). After that, the diversity increased again and reached a peak in the Campanian, and decreased a little in the Maastrichtian, the last stage age of Cretaceous.

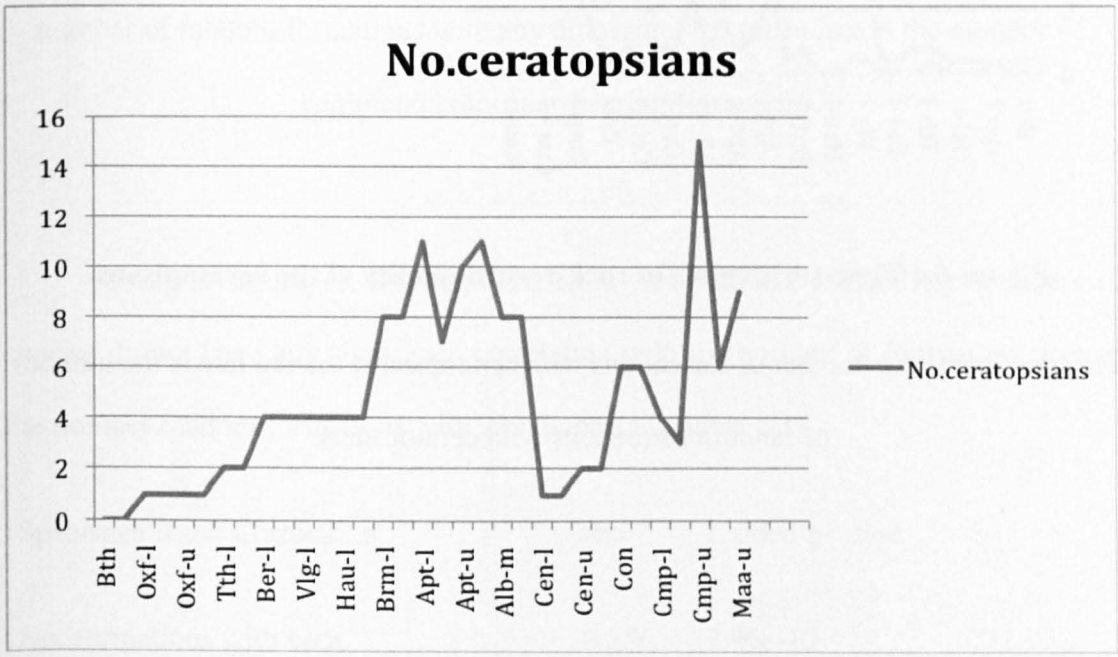

Figure 6.3 The diversity of ceratopsians in each time bin of Cretaceous and early Jurassic.

The blue line is the number of ceratopsians.

To assess the influence of the rock record on ceratopsian diversity, I collected

information on numbers of formations with ceratopsians. For the bad quality of some geological sites, for example, the age of some formations are ambiguous or contain several stages, so I randomise my data by computer to fit the unclearly dated formations to a fixed age. I found the curves of diversity and formations are similar. The most obvious difference is the number of formations with ceratopsians reaching a peak in the Maastrichtian, not Campanian (Fig 6.4).

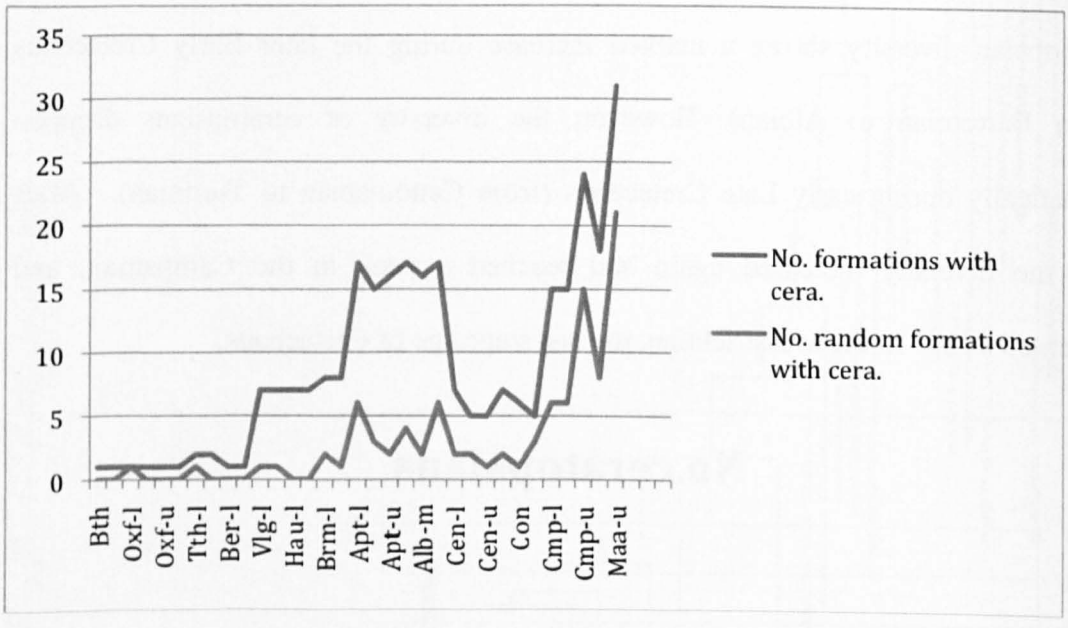

Figure 6.4 Time-series plots of rock-record quality of the ceratopisans.

The blue line is the number of formations with ceratopsians; the red line is the number of random formations with ceratopsians.

For comparing the data with all dinosaurs, I did some work on the rock-record quality of the dinosaurs during the period of the Late Jurassic to the end of the Cretaceous (Fig. 6.5). The formation curves are similar to that of ceratopsians.

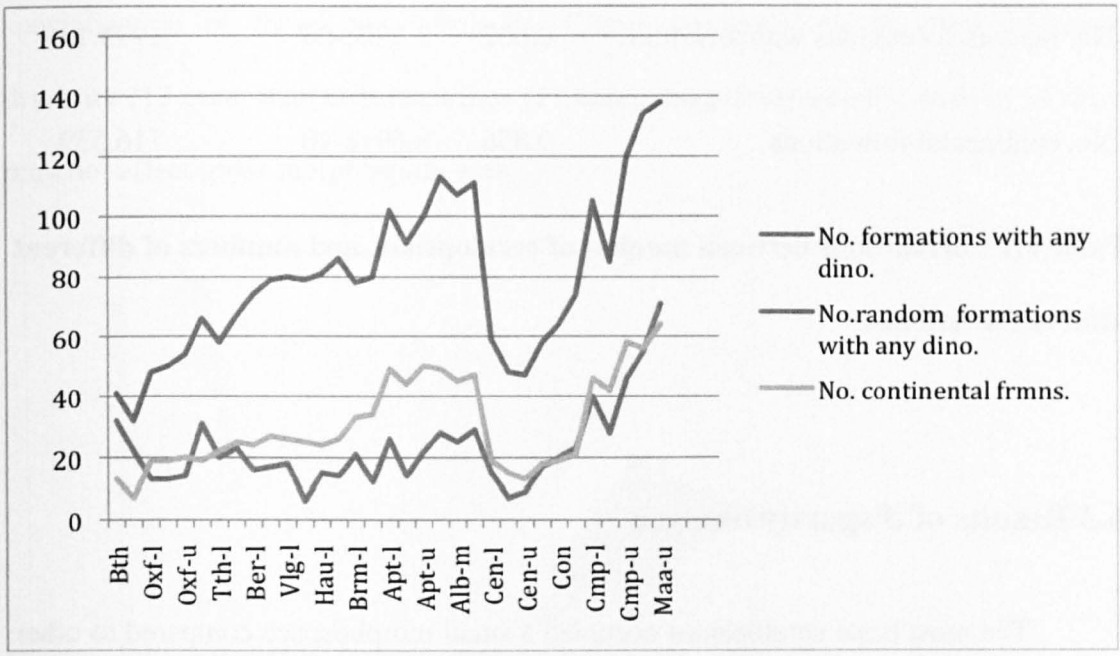

Figure 6.5 Time-series plots of rock-record quality of the dinosaurs.

The blue line is the number of formations with any dinosaurs; the red line is the number of random formations with any dinosaurs; the green line is the number of continental dinosaur-bearing formations.

Using R scripts (R Development Core Team 2008), I found the numbers of species do not have any significant correlation with the number of formations (except the number random formations with any dinosaurs) (table 6.1).

Spearman Rank Correlation	rho	2-sided p-value	S
No. formations with cera.	0.856	7.96e-10	711.932
No. formations with any dino	0.863	4.284e-10	680.095
No. random formations with cera	0.742	1.800e-06	1280.985

No. random formations with any dino.	0.602	3.380e-04	1973.149
No. continental formations	0.856	8.691e-10	716.539

Table 6.1 Correlations between number of ceratopsians and numbers of different kind of formations.

6.3 Results of disparity analysis

The most basal ceratopsians occupied a small morphospace compared to other groups. Similar to the phylogenetic results, I found that *Chaoyangosaurus* has a close morphospace distance from *Psittacosaurus*, while *Yinlong* is very close to basal neoceratopsians (Fig. 7.1). So the disparity study supports my previous hypothesis that *Yinlong* is a kind of basal neoceratopsian, not the most basal ceratopsian.

The disparity study shows the basal neoceratopsians occupied a larger amount of morphospace than did chasmosaurines and centrosaurines as a whole (Fig. 7.1), although basal neoceratopsians have lower taxonomic diversity (22 taxa) than ceratopsids (30 taxa including chasmosaurines and centrosaruines). This suggests a substantial reduction in overall morphospace occupied, or perhaps specialization in morphology, so overall morphospace occupied is reduced, but packing of taxa within those morphospace envelopes has increased.

The centrosaurines and chasmosaurines are the two major clades of ceratopsids. In the morphospace, these two clades occupied similar amounts of morphospace, but they are separated when viewed in all three dimensions (Figs. 6.6, 6.7, and 6.8). This means that they show similar amounts of morphological diversification, but in different areas of morphospace, suggesting divergence and

specialization of these two subclades. Chasmosaurines have higher taxonomic diversity (19 taxa) than centrosaurines (11 taxa), suggesting that the number of taxa may not affect gross morphospace area.

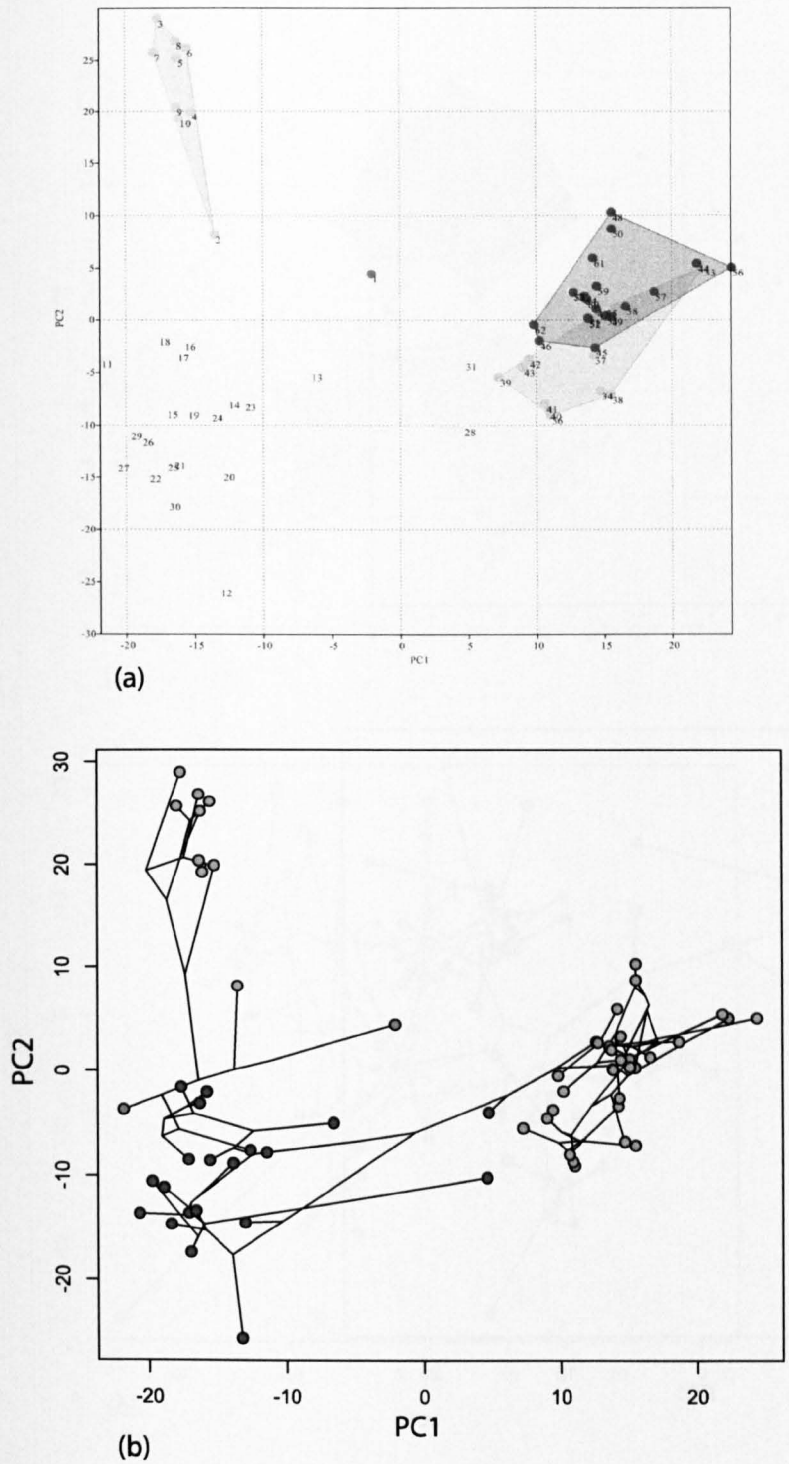

Figure 6.6 The morphospace (a) and phylomorphospace (b) of the ceratopsians, based on the first two principal coordinates (PC1 and PC2).

Red (a) and Purple (b) circle, Pachycephalosauria; Aqua (a) and darkseagreen (b) circles, the most basal ceratopsians; yellow (a) and tan (b) circles, basal neoceratopsians; number 11(a) and orange circle (b), *Yinlong downsi*; chartreuse (a) and deepskyblue (b) circles, centrosaurines; darkcyan (a) and limegreen (b) circles, chasmosaurines.

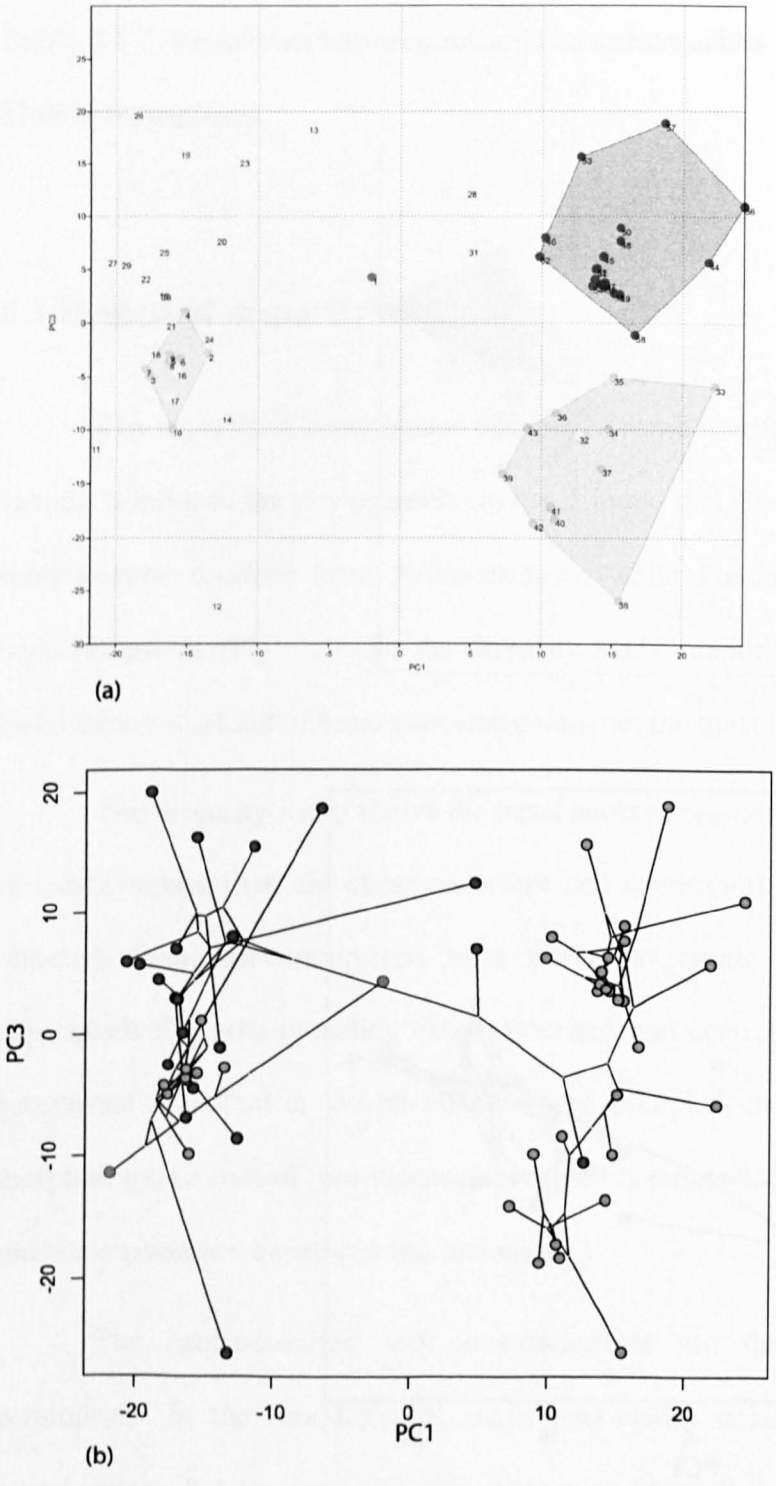

Figure 6.7 The morphospace (a) and phylomorphospace (b) of the ceratopsians, based on the first and third principal coordinates (PC1 and PC3).

Red (a) and Purple (b) circle, Pachycephalosauria; Aqua (a) and darkseagreen (b) circles, the most basal ceratopsians; yellow (a) and tan (b) circles, basal neoceratopsians; number 11(a) and orange circle (b), *Yinlong downsi*; chartreuse (a) and deepskyblue (b) circles, centrosaurines; darkcyan (a) and limegreen (b) circles, chasmosaurines.

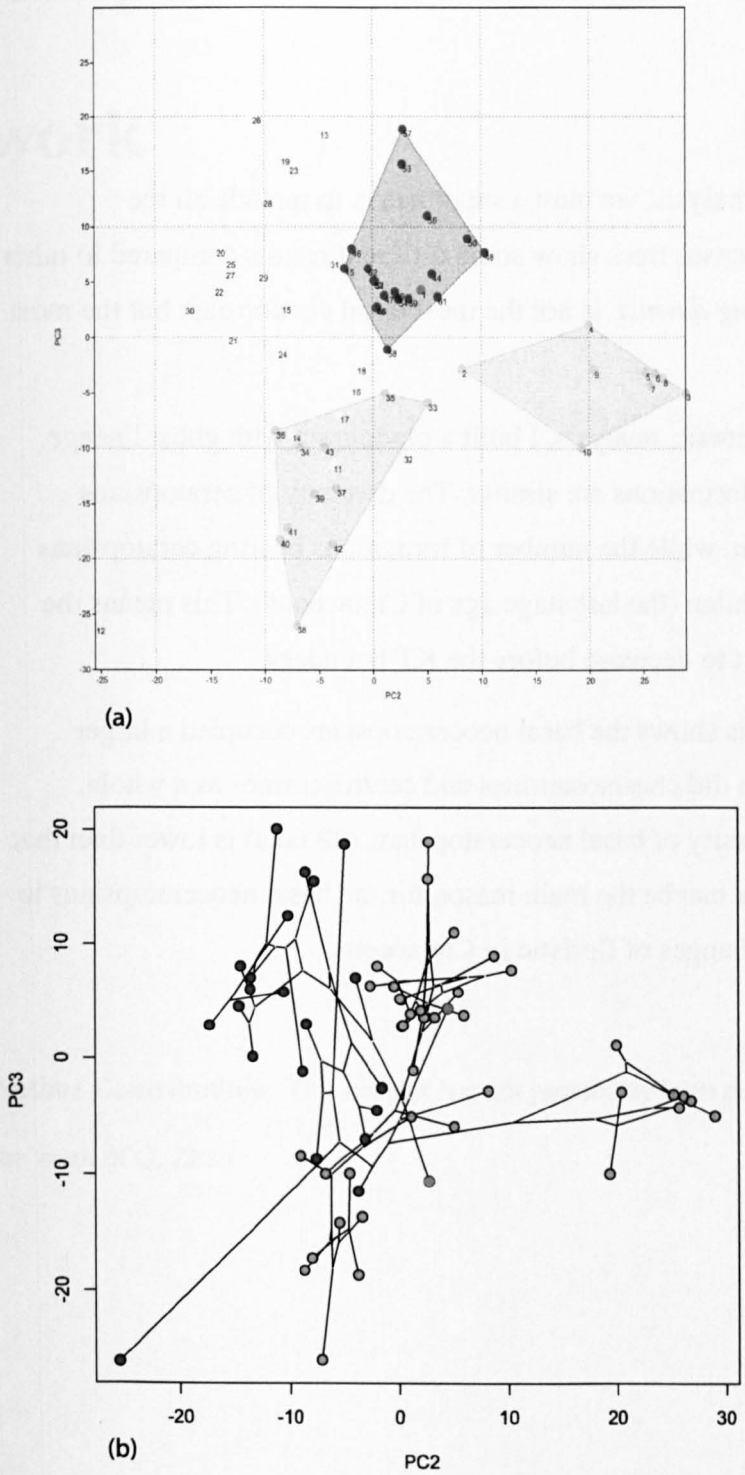

Figure 6.8 The morphospace (a) and phylomorphospace (b) of the ceratopsians, based on the second and third principal coordinates (PC2 and PC3).

Red (a) and Purple (b) circle, Pachycephalosauria; Aqua (a) and darkseagreen (b) circles, the most basal ceratopsians; yellow (a) and tan (b) circles, basal neoceratopsians; number 11(a) and orange circle (b), *Yinlong downsi*; chartreuse (a) and deepskyblue (b) circles, centrosaurines; darkcyan (a) and limegreen (b) circles, chasmosaurines.

6.3 Conclusion

In the phylogenetic analysis, we built a supermatrix to include all the ceratopsians. The strict consensus trees show some different results compared to other literatures, such as the *Yinlong downsi* is not the most basal ceratopsian, but the most basal Neoceratopsia.

Based on the phylogenetic analysis, I built a phylogram with ghost lineage. The curves of diversity and formations are similar. The diversity of ceratopsians reached a peak in Campanian, while the number of formations bearing ceratopsians reached its peak in Maastrichtian (the last stage age of Cretaceous). This means the diversity of ceratopsians start to decrease before the KT boundary.

This disparity analysis shows the basal neoceratopsians occupied a larger amount of morphospace than did chasmosaurines and centrosaurines as a whole, although the taxonomic diversity of basal neoceratopsians (22 taxa) is lower than that of ceratopsids (30 taxa). This maybe the main reason for the basal neoceratopsians to survival from the dramatic changes of floristic in Cretaceous.

Chapter 7 Conclusions and future work

Author Contributions: This chapter has not previously been published. All material herein is the work of Q. Zhao

7.1 Conclusions

In my PhD thesis, I carried out research on the evolution of ceratopsians through bone histology and numerical analysis. Based on numerous specimens of *Psittacosaurus lujiatunensis* in different ontogenetic stages, I carried out a bone histological study of ontogenetic growth in *Psittacosaurus lujiatunensis* and compared it with *Psittacosaurus mongoliensis*. Investigating the information in the bone thin sections, I found some interesting discoveries in dinosaur behaviour, such as posture shift and juvenile-only clusters. Numerical analyses on phylogeny, diversity and disparity show the macroevolution pattern of ceratopsians.

7.1.1 Key findings

The locomotion of *Psittacosaurus*

The mechanism of postural shift in *Psittacosaurus* is revealed by histological study. More than 15 thin sections were taken from the *Psittacosaurus lujiatunensis* juveniles (IVPP14341) to compare the forelimb and hindlimb bones. In the thin sections, the cortex is fibrolamellar bone with various vascular canals. The degree of vascularization is high, and only primary osteons can be observed in the thin sections. I found that forelimb bones, the humerus and radius, show a great number of radial vascular canals, whereas hindlimb bones, the femur and fibula, show many longitudinal and reticular vascular canals, but hardly any radial canals. This is evidence that the forelimbs, at least up to the age of three, showed more rapid growth than the hindlimbs, as radial vascular canals imply a faster grow rate than longitudinal vascular canals, based on observations of living birds. Further, the presence and relative abundance of primary osteons, two consequences of the initial porosity of

bone at the time of its deposition, are strongly related to bone growth rate. By comparing the vascular organizations in humeri and femora older than 3 years old, more reticular vascular canals were found in femora than humeri, which means the hindlimb grows faster than forelimb in this stage. Similar histological structures were also found in *Psittacosaurus mongoliensis*.

The transition from quadrupedality to bipedality appears to have occurred at about age 2. This is based on measurements of *Psittacosaurus lujiatunensis* individuals from hatchling stage to adult stage. I found that the ratio of forelimb to hindlimb length decreased from 0.851 to 0.668, but steadily and without any sudden transition. This also shows that the forelimb and hindlimb had different growth rates through the stages of ontogeny.

Juvenile-only clusters

Based on the detailed research on bone histology, I found the parental care specimen in Dalian Museum (Meng et al., 2004) is a fake fossil, the "adult" individual in that specimen is added to the slab of juvenile *Psittacosaurus*. So this specimen is just a juvenile-only cluster. Compared to the social behaviour in other groups of dinosaurs, the juvenile-only cluster is very common. IVPP V14341 is another *Psittacosaurus* juvenile-only cluster. Bone histology analysis confirms the IVPP V14341 is also a mix-aged cluster which has a 3-year old individual and five 2-year old individuals. This is also the first time to use bone histology to prove the present of mix-aged herd in dinosaurs.

Growth pattern in *P. lujiatunesis*

In the series of thin sections from *P. lujiatunensis*, I recognized five types of bone tissue and four histological ontogenetic stages, i.e., hatchling, juvenile, sub-adult, and adult. None of the specimens was fully-grown.

P. mongoliensis and *P. lujiatunensis* are similar in external morphology, but their growth patterns in bone histology show more differences. Erickson and Tumanova (2000) did some very clear histological work on *P. mongoliensis*. Compared with *P. lujiatunensis*, I found they have a similar growth pattern in the early stage, so there are just longitudinal vascular canals in femora in the first age, and similar proportions of reticular and longitudinal vascular canals at ages 1-4. But after age 5, *P. mongoliensis* has many reticular vascular canals, but *P. lujiatunensis* is totally different in that longitudinal vascular canals dominate the main cortex.

Numerical analysis of ceratopsians

According to the cladistic analysis, *Chaoyangsaurus youngi* is considered to be the most basal neoceratopsian, and *Yinlong downsi* is the most basal neoceratopsian instead of *Chaoyangsaurus youngi*. *Leptoceratops* and *Udanoceratops* are sister groups, and *Prenoceratops* lies just outside the clade of *Leptoceratops* and *Udanoceratops*. *Montanoceratops* lies outside the clade of *Bainocertaops*, *Leptoceratops*, *Udanoceratops*, and *Prenoceratops*.

Comparing a great deal of measurements on diversity and numbers of formations, I thought the plus ghost lineage diversity is meaningful to show the richness changes in ceratopsian dinosaurs. All the measurements show the diversity of ceratopsians reached a peak in the late Campanian and dropped in the last stage of the Cretaceous (Maastrichtian). This supports the idea that the major large-bodied

herbivorous ceratopsians endured about 5 Ma of decline in taxonomic diversity before their extinction.

In the disparity research, I discovered that the basal neoceratopsians occupied the largest morphospace compared to other groups. Similar to the phylogenetic results, I found that *Chaoyangosaurus* has a close morphospace distance from *Psittacosaurus*, while *Yinlong* is very close to basal neoceratopsians. So the disparity study supports my previous hypothesis that *Yinlong* is a kind of basal neoceratopsian, not the most basal ceratopsian.

Centrosaurines and chasmosaurines occupied similar amounts of morphospace, but they are separated when viewed in all three dimensions. Chasmosaurines have higher taxonomic diversity (19 taxa) than centrosaurines (11 taxa), suggesting that the number of taxa may not affect gross morphospace area.

7.2 Future work

Current work suggests that dinosaurs reached sexual maturity fast and sexual maturation occurred well before full adult size was reached—the primitive reptilian condition (Erickson et al., 2009; Erickson et al., 2007). I hope to establish, from bone thin sections, whether *Psittacosaurus* fits this pattern or not, and then use this information to compare with studies going on in North America on the later ceratopsians. The key question concerns the rate of growth to sexual maturity, taking account of overall body size, which increased in most later forms.

Based on the diversity research on ceratopsians, I want to determine how the rush of new plants and new animals affected the dinosaurs as they were increasingly marginalised. As angiosperms took over floras, there is minimal evidence that

dinosaurs adapted to these new sources of food. In fact, they seem to have continued feeding on gymnosperms, ferns, and the other plants they were already adapted to. Evidence for this comes from published references on analysis of dinosaur coprolites from the Late Cretaceous (Prasad et al., 2005) from plots of dinosaur and plant coevolution through the Cretaceous (Barrett and Willis 2001), and from a recent study of rates of evolution among dinosaur groups through the Cretaceous (Lloyd et al. 2008).

Appendix

I. Character Description

Ceratopsia

The 318 characters listed below are arranged in anatomical sequence, which come from Sereno 2000; Forster 1990a; Makovicky & Norell 2006; You & Dodson 2004; Ryan 2007; Averianov et al. 2006; Xu et al. 2002; Chinney & Horner 2007; Dodson et al. 2004; Sampson et al. 2010; Farke et al. 2011; and Wu et al. 2007, respectively, and some are modified.

1. Skull length (anterior margin of rostral-posterior margin of quadrate)/postcranial skeleton length (anterior margin of atlas to distal tip of tail): <15% (0); 20-30% (1). (Sereno 2000: 10; Makovicky & Norell 2006: 1; You & Dodson 2004:1; Xu et al. 2002: 1)

2. The breadth of the skull across the flaring jugal horns: less than skull length (anterior margin of rostral-posterior margin of quadrate) (0); exceeds skull length (1) (Averianov et al. 2006: 3)

3. Head shape in dorsal view: elongate, ovoid (0); or triangular, wide over jugals (1); rectangular (2) (Makovicky & Norell 2006: 2; partly Averianov et al. 2006: 2; Chinney & Horner 2007: 98; Xu et al. 2002: 2)

4. Preorbital length/skull length (anterior margin of rostral-posterior margin of quadrate): 30-35% (0); 36-40% (1); 40-50% (2); 50-70% (3); >75% (4) (modified from You & Dodson 2004: 2; Makovicky & Norell 2006: 4; Xu et al. 2002: 99; Chinney & Horner 2007: 100; Xu et al. 2002: 21)

5. External naris, position: low, adjacent to ventral border of premaxilla (0); high, separated by a flat area (1); extremely high, and posteriorly placed (2). (Sereno 2000: 2; You & Dodson 2004: 3).

6. External naris, shape: elliptical (0); round (1). (You & Dodson 2004: 4)

7. External naris, anteroposterior width: <10% skull length (0); >10% skull length (1). (Makovicky & Norell 2006: 19; You & Dodson 2004: 5)

8. Anterior end of the nasal (internarial bar) above (0); below and far anterior to the external naris (1). (Makovicky & Norell 2006: 14, Xu et al. 2002: 103)

9. Nares position close to buccal margin (0); dorsal, away from buccal margin (1); very far dorsal, level with upper part of orbit (2). (Makovicky & Norell 2006: 15; Chinney & Horner 2007: 111; Xu et al. 2002: 8)

10. External naris, size and position: small, restricted to dorsal one-third of snout (0); large, expanded to occupy most of the depth of the snout (1). (Dodson et al. 2004:2; Chinney & Horner 2007: 6; Sereno 2000: ampson 2)

11. Ventral border of external nares significantly below (0); about the level of (1); significantly above (2) lower rim of infratemporal fenestra. (Makovicky & Norell 2006: 16; Xu et al. 2002: 100; Chinney & Horner 2007: 7; Xu et al. 2002: 22)

12. Large depression excavating premaxilla anteroventral to naris absent (0); present (1). (Makovicky & Norell 2006: 17; Chinney & Horner 2007: 112)

13. Antorbital fossa: absent or reduced, less than 10% basal skull length (0); greater than 10% basal skull length and triangular (1). (Makovicky & Norell 2006: 23; You & Dodson 2004: 6; Chinney & Horner 2007: 18)

14. Antorbital fossa, shape: absent (0); subtriangular (1); oval (2). (Sereno 2000: 21; You & Dodson 2004: 7; Chinney & Horner 2007: 19, modified by Qi Zhao)

15. Additional antorbital fenestra size: pronounced, penetration of nasal cavity visible in lateral view (0); slight penetration, nasal cavity not visible in lateral view (1); absent (2). (You & Dodson 2004: 8; Sampson et al. 2010: 21; Forster 1990a: 15; Farke et al. 2011: 14; Sampson et al. 2010: 22; modified by Qi Zhao)

16. Orbit, orientation: directed rostrolaterally (0); directed laterally (1). (Sampson et al. 2010: 32)

17. Orbit diameter/skull length: >20% (0); <20% (1). (Makovicky & Norell 2006: 3; You & Dodson 2004: 9; Chinney & Horner 2007: 21; Sampson et al. 2010: 33)

18. Infratemporal fenestra, width: >10% skull length (0); <10% skull length (1). (Makovicky & Norell 2006: 35; You & Dodson 2004: 10; Chinney & Horner 2007: 26; Sampson et al. 2010: 52)

19. Infratemporal bar length: long, subequal to supratemporal bar (0); short, less than one-half supratemporal bar (1). (You & Dodson 2004: 11; Sereno 2000: 23)

20. Supratemporal fenestra, relation: separated (0); joined in midline (1); absent (2). (You & Dodson 2004: 12; Sereno 2000: 32)

21. Supratemporal fenestra, shape: oval (0); subtriangular (1); absent (2). (You & Dodson 2004: 13; Sereno 2000: 51; Sereno 2000: 52; Makovicky & Norell 2006: 29)

22. Frill fenestra: absent, solid frill (0); present, fenestrated near posterior margin (1). (You & Dodson 2004: 14; Makovicky & Norell 2006: 54; Sereno 2000: 55)

23. Dorsal edge of squamosal temporal bar curves medially at the posterior end, arcing confluently into posterior frill margin (0); dorsal edge of squamosal meets posterior margin of frill at acute angle (1). (Makovicky & Norell 2006: 54)

24. Rostral, size and shape: triangular in lateral view with short dorsal and ventral processes (0); enlarged with deeply concave posterior margin and hypertrophied dorsal and ventral processes (1); absent (2). (Dodson et al. 2004:1; Sampson et al. 2010: 1; Xu et al. 2002: 51)

25. Rostral, anterior margin in dorsal view: rounded (0); keeled with point (1). (You & Dodson 2004: 16; Makovicky & Norell 2006: 8; Sereno 2000: 11; Chinney & Horner 2007: 2; Xu et al. 2002: 5)

26. Rostral ventral (buccal) process: absent (0); present (1). (You & Dodson 2004: 18; Makovicky & Norell 2006: 7; Chinney & Horner 2007: 1; Xu et al. 2002: 4)

27. Tip of rostral low and level with maxillary tooth row (0); raised and dorsal to maxillary tooth row (1). (Makovicky & Norell 2006: 5; Xu et al. 2002: 117)

28. Rostral bone forming beak absent (0); present (1). (Makovicky & Norell 2006: 6; Chinney & Horner 2007: 99)

29. Rostral-nasal contact: absent (0); present (1). (Sereno 1987)

30. Premaxilla, shape in lateral view, except for the processes: longer than high (0); higher than long (1). (You & Dodson 2004: 19)

31. Relative height of premaxilla to orbit: low (0); deep (1). (You & Dodson 2004: 20; Makovicky & Norell 2006: 10; Chinney & Horner 2007: 11)

32. Shape of ventral border of premaxilla: ventrally convex (0); straight (1); concave (2). (You & Dodson 2004: 21; Chinney & Horner 2007: 12)

33. Premaxilla, depression anteroventral to naris: absent (0); present (1). (You & Dodson 2004: 22)

34. Convex buccal process anterior to maxillary tooth row formed by premaxilla or premaxilla and maxilla absent (0); present (1). (Makovicky & Norell 2006: 12; Farke et al. 2011: et al. 2011: 10)

35. Premaxilla–maxilla buccal margin relatively straight in ventral view, tooth rows/buccal margins converge anteriorly (0); buccal margin sinuous in ventral view, with premaxillary palatal region flaring widely anterior to tooth row (1). (You & Dodson 2004: 23; Makovicky & Norell 2006: 13; Xu et al. 2002: 100; Chinney & Horner 2007: 101)

36. Premaxilla-jugal contact: absent (0); present (1). (Sereno 1987)

37. Premaxillary septum, shape: subcircular (0); rostrally elongate (1); absent (2). (Dodson et al. 2004:4; Sampson et al. 2010: 4)

38. Premaxillary septum, nasal contribution: septum formed by premaxilla only (0); septum formed by premaxilla and nasal (1); absent (2). (Sampson et al. 2010: 5)

39. Premaxilla, thickened narial strut along posterior margin of the premaxillary septum: absent (0); present (1). (Dodson et al. 2004:5; Chinney & Horner 2007: 4; Sampson et al. 2010: 6; Holmes 1)

40. Premaxilla, narial strut orientation: rostrally inclined (0); posteriorly inclined (1); absent (2). (Dodson et al. 2004:6; Sampson et al. 2010: 7)

41. Premaxilla, bony flange on posterior margin of narial strut: absent (0); present (1). (Dodson et al. 2004:7; Sampson et al. 2010: 8)

42. Premaxilla, septal flange length: spans entire caudal margin of narial strut (0);

restricted to ventral portion of narial strut (1); abstent (2). (Sampson et al. 2010: 9)

43. Premaxilla, interpremaxillary fossa perforating premaxillary septum: absent (0); present (1). (Dodson et al. 2004:8; Sampson et al. 2010: 11)

44. Premaxilla, recess in ventral portion of septum: absent (0); present (1). (Dodson et al. 2004:9; Sampson et al. 2010: 16)

45. Premaxilla, accessory strut in septal fossa: no accessory strut (0); strut present (1). (Sereno 2000: ampson 12; Holmes 4)

46. Premaxilla, size of recess in septum: small, slight in-pocketing along ventral aspect of septal fossa (0); large, deeply recessed into premaxilla (1); absent (2). (Dodson et al. 2004: 10)

47. Premaxilla, premaxillary (narial) process extending into the external naris from the posteroventral margin of the premaxillary septum: absent (0); present (1). (Dodson et al. 2004:11; Sampson et al. 2010: 13; Holmes 6; Foster 21)

48. Premaxilla, triangular process shape: square (0); pinched and triangular with concave facets (1); absent (2). (Sampson et al. 2010: 14)

49. Premaxilla, recess on lateral surface of the premaxillary (narial) process: absent (0); present (1). (Dodson et al. 2004:12; Sampson et al. 2010: 15)

50. Premaxilla, ventral expansion of the posteroventral oral margin: absent, posteroventral oral margin of premaxilla level with alveolar margin of the maxilla (0); present, expanded ventrally to extend well below alveolar margin of the maxilla (1). (Dodson et al. 2004:13 ; Sampson et al. 2010: 17; Farke et al. 2011: 9)

51. Premaxilla, posterior tip of posteroventral process inserts into an embayment in the nasal and is surrounded by the nasal: present (0); absent (1). (Dodson et al. 2004:14; Sampson et al. 2010: 18; Forster 1990a: 7; Farke et al. 2011: 11)

52. Premaxilla, forked distal end of posteroventral process: absent (0); present (1). (Dodson et al. 2004:15; Sampson et al. 2010: 19; Forster 1990a: 7; Farke et al. 2011: 12)

53. Premaxilla-nasal contact in dorsal view: premaxillae insert between nasal (0); nasals insert between premaxillae (1). (Sampson et al. 2010: 20; Farke et al. 2011: 13)

54. A process projecting into the interpremaxillary fenestra: absent (0); present (1). (Wu et al. 2007: 76)

55. External antorbital fenestra, size: large, 20% or more length of body of maxilla (0); greatly reduced to less than 10% length of body of maxilla, or absent (1). (Dodson et al. 2004:16; Sampson et al. 2010: 23; Farke et al. 2011: 16)

56. Eminence or tubercle on the rim of the buccal emargination of the maxilla near the junction with the jugal absent (0); present (1). (Makovicky & Norell 2006: 24; Xu et al. 2002: 24)

57. Premaxilla–prefrontal contact absent (0); present (1). (You & Dodson 2004: 23; Makovicky & Norell 2006: 11; Xu et al. 2002: 102)

58. Maxilla, relation of alveolar margin to rostral edentulous margin: edentulous portion maxilla elevated above level of alveoli (0); at same level (1). (Sampson et al. 2010: 24)

59. Maxilla, diastema on rostral maxilla: present (0); absent (1). (Sampson et al. 2010: 25)

60. Maxilla, maxillary cavity: absent (0); present (1). (Sampson et al. 2010: 26)

61. Maxilla, edentulous maxillary/dentary margin length: 2 tooth spaces (0); 4 or 5 tooth spaces (1). (You & Dodson 2004: 24; Sereno 2000: 16; Makovicky & Norell 2006: 55)

62. Dentigerous margin of maxilla: straight (0); ventrally concave (1). (You & Dodson 2004: 25; Makovicky & Norell 2006: 22; Chinney & Horner 2007: 17)

63. Maxillary fossa: absent (0); present (1). (Sereno 2010: 8)

64. Maxillary protuberance: absent (0); present (1). (Sereno 1987)

65. External nares horn: absent (0); small (1); large (2). (You & Dodson 2004: 26; Makovicky & Norell 2006: 18; Sereno 2000: 50; Chinney & Horner 2007: 5)

66. Nasal horn core, position: posterior to posterior margin of external nares (0); dorsal to posterior margin of external nares (1); absent (2). (Wu et al. 2007:74; You & Dodson 2004: 27; Sereno 2000: 65)

67. Transversely arched vascular trace across the anterior surface of the nasal horn core: absent (0); present (1). (Wu et al. 2007:75)

68. Nasal, ornamentation: absent (0); horncore (1); pachyostotic boss (2). (Dodson et al. 2004: 17; Sampson et al. 2010: 28; Mcdonald 1; Farke et al. 2011: 20)

69. Nasal, ornamentation position: centered posterior or posterodorsal to internal naris (0); shifted forward, centered dorsal or rostrodorsal to endonaris (1); absent (2). (Dodson et al. 2004:18; Sampson et al. 2010: 29)

70. Nasal, horncore length: small, length of horncore less than 15% basal skull length (0); moderate to large, length of horncore 20% or more of basal skull length (1); absent (2). (Dodson et al. 2004:19)

71. Narial spine of nasal, a pronounced tablike process projecting rostrally into the nasal vestibule from the posterior narial margin: absent (0); present (1). (Ryan 2007: 12, Mcdonald 5; Sampson et al. 2010: 30; Farke et al. 2011: 22)

72. Facial skeleton, dorsoventral depth in orbital region: deep, alveolar process of maxilla entirely visible (0); shallow, alveolar process of maxilla obscured by jugal (1). (Sampson et al. 2010: 31)

73. Palpebral, articulation: rod-like, articulates with prefrontal only at its base and projects across dorsal orbit, ligamentous attachment (0); blocky, fully fused into dorsal orbital margin, sutural articulation with prefrontal and frontal (1). (You & Dodson 2004: 28; Makovicky & Norell 2006: 25; Chinney & Horner 2007: 23; Sampson et al. 2010: 43; Farke et al. 2011: 32)

74. Palpebral, orientation of posterior (medial) margin: posterolateral (0); transverse (laterally divergent) (1). (Sereno 2010: 17)

75. Palpebral, antorbital buttress: absent (0); present (1). (Sampson et al. 2010: 44; Farke et al. 2011: 33)

76. Palpebral, extent of antorbital buttress: present along only anterodorsal portion of orbit (0); present along entire anterior portion of orbit (1). (Sampson et al. 2010: 45; Farke et al. 2011: 34)

77. Lacrimal, size: large, forms 50% or more of the anterior orbital margin (0); small, forms 40% or less of the anterior orbital margin (1). (Dodson et al. 2004:20; Chinney & Horner 2007: 22; Sampson et al. 2010: 34)

78. Jugal lateral expansion: absent (0); slightly developed (1); well developed, jugal horn (2). (You & Dodson 2004: 29; Sereno 2000: 3; Makovicky & Norell 2006: 27; Chinney & Horner 2007: 102)

79. Jugal lateral expansion, position: from midsection (0); from posterior end (1). (You & Dodson 2004: 30)

80. Jugal lateral expansion, direction: laterally (0); lateroventrally (ventral to M tooth row) (1). (You & Dodson 2004: 31; Makovicky & Norell 2006: 27)

81. Jugal infraorbital ramus, relative dorsoventral width, compared to infratemporal ramus: less than (0); subequal to more than (1). (You & Dodson 2004: 32; Sereno 2000: 5; Makovicky & Norell 2006: 28)

82. Jugal fossa: absent (0); present (1). (Sereno 2010: 5)

83. Jugal-lacrimal contact: reduced (0); expanded (1). (You & Dodson 2004: 33; Makovicky & Norell 2006: 26; Chinney & Horner 2007: 49; Sampson et al. 2010: 48)

84. Jugal (jugal-epijugal) crest: absent (0); present (1). (You & Dodson 2004: 34; Sereno 2000: 4)

85. Jugal/epijugal crest, development: low (0); pronounced (1). (You & Dodson 2004: 35; Sereno 2000: 24)

86. Jugal infratemporal flange: absent (0); present, contacts process of squamosal below the infratemporal fenestra (1). (Dodson et al. 2004:27; Sampson et al. 2010: 47; Farke et al. 2011: 36)

87. Supracranial cavity complex: absent (0); present, supracranial cavities narrow and shallow, do not underlie supraorbital ornamentation (1); present, supracranial cavities broad, underlie supraorbital ornamentation and may be confluent with extensive cornual sinuses (2). (Dodson et al. 2004:29; Forster 1990a: 123; Sampson et al. 2010: 36; Farke et al. 2011: 23)

88. Epijugal: absent (0); present (1). (You & Dodson 2004: 36; Makovicky & Norell 2006: 29; Sereno 2000: 31; Chinney & Horner 2007: 52; Xu et al. 2002: 10)

89. Epijugal, position: along dorsal edge of horn (epijugal trapezoidal) (0); capping end of horn (epijugal conical) (1); absent (2). (You & Dodson 2004: 37; Makovicky & Norell 2006: 30)

90. Shape of epijugal: crest-shaped (0); conical (1); absent (2). (Chinney & Horner 2007: 53)

91. Epijugal length: long (0); hyperlong (1); short (2); absent (3). (Sampson et al. 2010: 50)

92. Quadratojugal-squamosal contact: absent (0); present (1). (Sampson et al. 2010: 51)

93. Quadratojugal, shape: mediolaterally flattened (0); transversely expanded and triangular in coronal section (1); triangular in coronal section, but with slender anterior prong articulating with jugal (2). (You & Dodson 2004: 38; Makovicky & Norell 2006: 40; Chinney & Horner 2007: 54)

94. Quadratojugal, exposure in lateral view: large (0); reduced, still visible in lateral view (1); invisible laterally (2). (You & Dodson 2004: 39)

95. Quadratojugal, position of contact with jugal and quadrate: jugal, quadratojugal, quadrate contact in an anterior to posterior order (0); jugal, quadratojugal, quadrate contact in a lateral to medial order (1). (Dodson et al. 2004:28)

96. Postorbital, shape: inverted and L-shaped (0); triangular and platelike (1). (You & Dodson 2004: 40; Makovicky & Norell 2006: 32; Chinney & Horner 2007: 28; Xu et al. 2002: 11)

97. Postorbital, dorsal part: rounded and overhanging lateral edge of supratemporal fenestra (0); with concave dorsal shelf bordering supratemporal fenestra (1). (You & Dodson 2004: 41; Makovicky & Norell 2006: 33)

98. Postorbital, contribution to upper bar of infratemporal fenestra: participate in margin (0); much reduced or excluded from margin (1); jugal-squamosal contact very wide and postorbital situated far from fenestra (2). (You & Dodson 2004: 42; Makovicky & Norell 2006: 34; Sereno 2000: 30; Chinney & Horner 2007: 30; Sampson et al. 2010: 42; Xu et al. 2002: 12)

99. Postorbital and supratemporal bars, maximum width: narrow, bar-shaped (0); broad, strap-shaped (1); very broad, plate-shaped (2). (You & Dodson 2004: 43; Sereno 2000: 22)

100. Postorbital posterior process, extension along supratemporal bar: partial (0); complete (1). (Sereno 2010)

101. Postorbital horn: absent (0); present (1). (You & Dodson 2004: 44; Sereno 2000: 72; Makovicky & Norell 2006: 31; Chinney & Horner 2007: 25)

102. Postorbital, supraorbital ornamentation in adult: absent (0); present (1). (Dodson et al. 2004: 21; Sampson et al. 2010: 35)

103. Postorbital, supraorbital ornamentation: horncore (0) rugose boss (1); absent (2). (Dodson et al. 2004:22; Farke et al. 2011: 25)

104. Postorbital, position of supraorbital ornamentation: centered rostrodorsal or dorsal to orbit (0); centered posterodorsal or posterior to orbit (1); absent (2). (Dodson et al. 2004: 23; Sampson et al. 2010: 37; Farke et al. 2011: 26)

105. Postorbital, orientation of supraorbital horncore base: dorsally directed (0); dorsolaterally directed (1); absent (2). (Sampson et al. 2010: 38; Farke et al.

2011: 27)

106. Form of postorbital ornamentation: conical horncore with rounded base and pointed apex; height at least three times as long as rostroposterior basal length (0); pyramidal horncore with approximately a 1:1 ratio of height to rostroposterior basal length (1); horncore longer rostroposteriorly than high, with rounded apex (2); absent (3). (Ryan 2007: 14; Farke et al. 2011: 24)

107. Postorbital, length of supraorbital horncore: elongate, greater than 35% basal skull length (0); short, less than 15% basal skull length (1); absent (2). (Dodson et al. 2004:24; Sampson et al. 2010: 39; Farke et al. 2011: 28)

108. Postorbital, curvature of supraorbital horncore in lateral view: posteriorly recurved (0); rostrally curved (1); straight (2); absent (3). (Dodson et al. 2004:25; Sampson et al. 2010: 40; Farke et al. 2011: 29)

109. Postorbital, curvature of supraorbital horncore in rostal view: medially recurved (0); laterally curved (1); straight (2); absent (3). (Sampson et al. 2010: 41)

110. Prefrontal-prefrontal contact: absent (0); present (1); absent (2). (Dodson et al. 2004:26; Chinney & Horner 2007: 27; Farke et al. 2011: 31)

111. Supratemporal bar, orientation (dorsal view): parasagittal (0); posteriorly divergent at an angle of approximately 15° (1). (Sereno 1987, 2010)

112. Parietal-frontal contact: flat (0); depressed (1); frontal fontanelle (2). (You & Dodson 2004: 45; Makovicky & Norell 2006: 51; Chinney & Horner 2007: 103; Sampson et al. 2010: 55; Farke et al. 2011: 38)

113. Frontal, contribution to orbital margin: present (0); absent (1). (Dodson et al. 2004:30; Sampson et al. 2010: 53)

114. Frontal, contribution to supratemporal fenestra: present (0); absent (1). (Sampson et al. 2010: 54)

115. Frontal fontanelle, shape: rostroposteriorly long and uniformly narrow transversely (0); keyhole shaped with a broad rostal half (1); broadly oval to circular (2); absent (3). (Dodson et al. 2004:31; Sampson et al. 2010: 56; Farke et al. 2011: 39)

116. Frontal, contribution to exit for c.n. I: present (0); absent, enclosed entirely by ossifications of the interorbital septum (1). (Dodson et al. 2004: 53)

117. Postorbital horncore shape: elongate with pointed apex and round to oval base (0); pyramidal with rounded apex, at least as tall as base is long (1); rounded apex, base longer than horn is tall (2); absent (3). (Ryan 2007: 16)

118. Postorbital ornamentation height: short, less than 40% length of face (0); long, greater than 60% length of face (1); absent (2). (Ryan 2007: 17)

119. Position of base of postorbital horncore (adult; Lehman, 1996; Holmes et al., 2001) posterior to orbit (0); over or anterior to orbit (1); absent (2). (Ryan 2007: 18)

120. Sagittal crest, heigh: low and rounded (0); blade-shaped (1). (You & Dodson 2004: 46; Sereno 2000: 60)

121. Parietosquamosal shelf: absent (0); present (1). (You & Dodson 2004: 47; partial of Sereno 2000: 54; Xu et al. 2002: 45)

122. Distinctive indentation on midline of the posterior parietals present (0); absent (1). (Makovicky & Norell 2006: 55; Xu et al. 2002: 25)

123. Parietosquamosal shelf, composition: parietal and squamosal equal (0); squamosal dominate (1); parietal dominates (2). (You & Dodson 2004: 48; Sereno 2000: 33)

124. Parietosquamosal frill: absent (0); parietal frill less than 70% of basal length of skull (1); more than 70% of basal length (2). (You & Dodson 2004: 49; Makovicky & Norell 2006: 52; partial Sereno 2000: 54; Chinney & Horner 2007: 31; Sampson et al. 2010: 69)

125. Parietosquamosal frill, location of maximum transverse width: caudally, at rear margin of frill (0); rostrally, in association with proximal half of frill (1); widest part in middle or frill relatively equal in width (2). (Sampson et al. 2010: 70)

126. Parietosquamosal frill, length relative to basal skull length: elongate, 0.80 or more (0); shortened, 0.70 or less (1). (Dodson et al. 2004: 32)

127. Parietosquamosal frill, marginal undulations: absent (0); present (1). Gilmore (1917). (Dodson et al. 2004: 33; Sampson et al. 2010: 82)

128. Parietosquamosal contact, shape in lateral view: straight (0); curved, medially concave (1). (Sampson et al. 2010: 65; Farke et al. 2011: 45; Forster 1990a: 119)

129. Temporal process of squamosal simple (0); deeply bifurcate around temporal process of postorbital (1). (Makovicky & Norell 2006: 37; Xu et al. 2002: 114; Chinney & Horner 2007: 33)

130. Parietal shelf, inclination: horizontal (0); posterodorsally (1). (You & Dodson 2004: 50; Sereno 2000: 34)

131. Parietal, width: subequal to dorsal skull roof (0); much wider than dorsal skull roof (1). (You & Dodson 2004: 51; Sereno 2000: 53)

132. Parietal, overall shpe: nearly straight along midline in lateral view and gently arched from side to side (0); "saddle-shaped," dorsally concave in lateral view with upturned caudal margin, and arched strongly from side to side (1). (Sampson et al. 2010: 72)

133. Parietal, imbrication effect on lateral margin of frill in adults: absent (0); present (1). (Dodson et al. 2004:34; Sampson et al. 2010: 83; Farke et al. 2011: 52)

134. Parietal fenestra: absent (0); present (1) (Mcdonald 15; Chinney & Horner 2007: 35; Sampson et al. 2010: 73)

135. Parietal fenestra, orientation: long axis directed transversely (0); long axis directed axially (1); axial and transverse axes equal (2); absent (3). (Dodson et al. 2004:38; Sampson et al. 2010: 80)

136. Parietal fenestra, maximum proximodistal diameter: 40% or less total parietal length (0); 45% or more total parietal length (1); absent (2). (Ryan 2007: 24; Dodson et al. 2004:39; Sampson et al. 2010: 81)

137. Parietal, accessory fenestra medial to the anterior end of the infratemporal fenestra: absent (0); present (1). (Dodson et al. 2004: 40)

138. Parietal, parietal sulci: absent (0); present (1). (Sampson et al. 2010: 71)

139. Parietal, median bar: narrow and straplike, width less than 0.05 total parietal length (0); wide, 0.15 or more total parietal length (1). (Dodson et al. 2004:41; Sampson et al. 2010: 76; Farke et al. 2011: 50)

140. Parietal, relative rostrocaudal depth of broad transverse bar: subequal medial to lateral (0); tapering so that the narrowest point occurs medially (1). (Sampson et al. 2010: 77)

141. Parietal, anterior extent on dorsum of skull relative to occipital condyle: rostral end of parietal located will in front of occipital condyle (0); rostral end of parietal lies directly over occipital condyle (1). (Sampson et al. 2010: 57; Farke et al. 2011: 40)

142. Parietal, concave median embayment on caudal margin: absent (0); present (1). (Sampson et al. 2010: 66; Farke et al. 2011: 46)

143. Parietal epoccipitals, number per side: one to three (0); six to eight (1); absent (2). (Dodson et al. 2004:46; Farke et al. 2011: 57; Sampson et al. 2010: 93)

144. Parietal epoccipital, most median epoccipital (locus 1) developed into a curved process with pronounced external sulci and ridges: absent (0); present (1). (Ryan 2007: 28; Dodson et al. 2004:47; Farke et al. 2011: 58; Sampson et al. 2010: 96)

145. Epiparietal, shape of locus P2: low D-shaped process, wider than long (0); elongate flattened process or spike, longer than wide (1); absent (2); (Sampson et al. 2010: 97; Farke et al. 2011: 59)

146. Parietal epoccipital, orientation at locus 1 relative to parietal: dorsal to rostrally directed (0); posteriorly directed (1); absent (2). (Dodson et al. 2004: 48)

147. Orientation of epoccipital at locus 1: posteriorly directed (0); dorsally directed (1); rostrally directed (pronounced anterior curl) (2); absent (3). (Ryan 2007: 29; after Sampson et al. 2010: 1995)

148. Parietal epoccipital, locus 2 developed into a curved process, with pronounced external sulci and ridges: absent (0); present (1). (Ryan 2007: 30; Dodson et al. 2004: 49)

149. Parietal epoccipital, orientation at locus 2: posteriorly directed from and perpendicular to parietal margin (0); medially directed, come off the parietal at an

angle (1); absent (2). (Dodson et al. 2004:50)

150. Parietal epoccipital, locus 3 modified into a large hornlike process: absent (0); present (1). (Ryan 2007: 31 32; Dodson et al. 2004: 51)

151. Rostroposterior width of posterior parietal ramus behind parietal fenestrae: relatively wide, ≥20% of total parietal length (0); narrow and straplike, width ≤10% of parietal length (1). (Ryan 2007: 25)

152. Parietal, median bar, transverse width: relatively wide, 15% of total parietal length (0); narrow and straplike, 10% of parietal length (1). (Ryan 2007: 26; Sampson et al. 2010: 79; Farke et al. 2011: 51)

153. Parietal, shape of concave median embayment: (0) shallow, restricted to center of margin; (1) shallow, entire transverse bar is a V-shaped embayment; absent (2). (Sampson et al. 2010: 67; Farke et al. 2011: 47)

154. Parietal, rim on medial margin of dorsotemporal fenestra: (0) absent; (1) present, well-defined, laterally projection rim ddefines medial margin of fenestra (Sampson et al. 2010: 74; Farke et al. 2011: 48)

155. Number of loci for epoccipitals on parietal rami lateral to the midline margin (this study): none (0); 3–5 (1); 6–8 (2). (Ryan 2007: 27)

156. Epoccipitals on parietal and squamosal: absent (0); present (1). (Dodson et al. 2004:42; Chinney & Horner 2007: 44)

157. Epoccipital crossing squamosal-parietal contact: absent (0); present (1). (Dodson et al. 2004: 43)

158. Epoccipitals, pattern of fusion to frill margin: occurs from anterior to posterior (0); occurs from posterior to anterior (1); absent (2). (Dodson et al. 2004: 44)

159. Shape of squamosal in lateral view: sub triangular (0); T-shaped (1) expanded both rostrocaudally and dorsoventrally as part of the frill. (You & Dodson 2004: 52; Makovicky & Norell 2006: 36; Sereno 2000: 59; Chinney & Horner 2007: 32)

160. Squamosal epoccipital, shape: crescentic or ellipsoidal (0); triangular (1); absent (2). (Dodson et al. 2004:45; Sampson et al. 2010: 87; Farke et al. 2011: 54)

161. Squamosal epoccipital, number per side: three to five (0); six or more (1); absent (2). (Farke et al. 2011: 55)

162. Squamosal, end of anterior process, position on postorbital: lateral (0); dorsal (1). (Sereno 2010)

163. Squamosal, postquadratic posteroventral process: absent (0); present (1). (You & Dodson 2004: 53)

164. Squamosal, posterior expansion: absent or very slight (0); present (1). (Sampson et al. 2010: 58)

165. Squamosal, length relative to parietal: equal or subequal in length (0); squamosal much shorter than parietal (1). (Dodson et al. 2004: 35; Sampson et al. 2010: 60)

166. Squamosal forms part of posterior margin of frill: present (0); absent (1). (Sampson et al. 2010: 61)

167. Squamosal, rostromedial lamina forming the posterolateral floor of supratemporal fossa: absent (0); present (1). (Dodson et al. 2004: 36; Sampson et al. 2010: 62; Farke et al. 2011: 42)

168. Shape of medial margin of squamosal: straight (0); posterior portion stepped-up relative to anterior portion (1). (Ryan 2007: 21)

169. Squamosal-quadrate contact: socketlike cotylus on squamosal for ball-like quadrate head (0); elongate groove on squamosal to receive lamina of quadrate (1). (Dodson et al. 2004: 37; Sampson et al. 2010: 63; Farke et al. 2011: 43)

170. Squamosal, thickened, rounded swelling along medial margin: absent, lateral surface of squamosal flat to slightly convex (0); present, lateral surface of squamosal slightly concave (1); (Forster 1990a: 90; Sampson et al. 2010: 64; Farke et al. 2011: 44).

171. Squamosal, posterior edge: angled anteromedially (0); or posteromedially, contributes lateral portion of frill margin (1). (Makovicky & Norell 2006: 38; Xu et al. 2002: 131)

172. Temporal bars of squamosals parallel (0); posteriorly divergent (1). (Makovicky & Norell 2006: 39)

173. Frill posterior margin: straight or wavy (0); round and convex (1). (You et al. 2004: 54)

174. Epioccipital ossification/frill scallops: absent (0); present (1). (You & Dodson 2004: 55; Makovicky & Norell 2006: 56)

175. Quadrate shaft: rostrally convex in lateral view (0); straight (1). (You & Dodson 2004: 56; Makovicky & Norell 2006: 41; Chinney & Horner 2007: 55)

176. Quadrate shaft, rostroposterior width: broad (0); narrow (1). (You & Dodson 2004: 57; Sereno 2000: 25)

177. Articular proportions: one half or less of quadrate articulation (0); more than 1/2 (1). (Chinney & Horner 2007: 70)

178. Palatal extension of premaxillae, form: flat (0); vaulted dorsally (1). (You & Dodson 2004: 58; Makovicky & Norell 2006: 9; Sereno 2000: 6; Chinney & Horner 2007: 9; Xu et al. 2002: 6)

179. Position of choana on palate: anterior to maxillary tooth row (0); level with maxillary tooth row (1). (You & Dodson 2004: 59; Makovicky & Norell 2006: 20; Chinney & Horner 2007: 8)

180. Palatal extensions of maxillae: separated by vomers at anterior border for the internal choanae (0); contact each other anterior to choanae (1). (You & Dodson 2004: 60; Makovicky & Norell 2006: 21; Chinney & Horner 2007: 15)

181. Palatine, elongate parasagittal process: absent (0); present (1). (You & Dodson 2004: 61; Makovicky & Norell 2006: 42)

182. Ectopterygoid in palatal view: exposed (0); reduced or concealed (1). (You & Dodson 2004: 62; Makovicky & Norell 2006: 4; Chinney & Horner 2007: 20)

183. Ectopterygoid-jugal-maxilla contact: ectopterygoid-jugal contacts (0); ectopterygoid reduced and restricted to contact with M (1). (You & Dodson 2004: 63; Makovicky & Norell 2006: 44; Chinney & Horner 2007: 51; Sampson et al. 2010: 109)

184. Pterygopalatine foramen (modified suborbital fenestra) large (0); diminutive (1). (Makovicky & Norell 2006: 45)

185. Ventral ridge on mandibular process of pterygoid defining eustachian canal: absent (0); present (1). (You & Dodson 2004: 64; Makovicky & Norell 2006: 46; Chinney & Horner 2007: 10)

186. Pterygoid-maxilla contact at posterior end of tooth row: absent (0); present (1). (You & Dodson 2004: 65; Makovicky & Norell 2006: 47; Chinney & Horner 2007: 16)

187. Prominent posterior midline process on pterygoid absent (0); present (1). (Makovicky & Norell 2006: 48; Xu et al. 2002: 106)

188. Pterygoid mandibular process short (0); long, extending well below maxillary tooth row (1). (Makovicky & Norell 2006: 49; Xu et al. 2002: 107; Chinney & Horner 2007: 114)

189. Pterygoid mandibular process formed only by pterygoid (0); jointly by pterygoid and ectopterygoid (1). (Makovicky & Norell 2006: 50; Xu et al. 2002: 108; Chinney & Horner 2007: 115)

190. Basioccipital: contributes to foramen magnum (0); forms 2/3 or more of the occipital condyle (1); forms less than 2/3 (2). (You & Dodson 2004: 66; Makovicky & Norell 2006: 57; Sereno 2000: 35; Chinney & Horner 2007: 36)

191. Basioccipital, contribution to basal tubera: exclude by basisphenoid and limited to occipital midline (0); basioccipital tubera present (1). (You & Dodson 2004: 67; Makovicky & Norell 2006: 58; Chinney & Horner 2007: 37)

192. Basioccipital, contribution to occipital condyle: large, forms more than one-third of condyle (0); reduced, forms ventral one-third of condyle only (1). (Dodson et al. 2004:52; Sampson et al. 2010: 104)

193. Basipterygoid process, orientation: anterior (0); ventral (1); posteroventral (2). (You & Dodson 2004: 68; Makovicky & Norell 2006: 59; Chinney & Horner 2007: 39)

194. Basal tubera-basioccipital relation: Basal tubera flat, in plane with basipterygoid plate (0); everted posterolaterally, forming lip beneath occipital condyle (1). (You & Dodson 2004: 69; Makovicky & Norell 2006: 60; Chinney & Horner 2007: 38)

195. Notch between posteroventral edge of basisphenoid and base of basipterygoid process: deep (0); notch shallow and base of basipterygoid process close to basioccipital tubera (1). (You & Dodson 2004: 70; Makovicky & Norell 2006: 61; Chinney & Horner 2007: 40)

196. Exoccipital, exits for cranial nerves in exoccipital: three foramina (0); with two foramina (1). (You & Dodson 2004: 71; Makovicky & Norell 2006: 62; Chinney & Horner 2007: 45; Sampson et al. 2010: 107)

197. Exoccipital-quadrate relation: separated by ventral flange of squamosal (0); in contact (1). (You & Dodson 2004: 72; Makovicky & Norell 2006: 63; Chinney & Horner 2007: 46)

198. Exoccipital, number of exits for c.nn. X, XI, XII: three (0); two (1). (Dodson et al. 2004:55)

199. Paroccipital process length: less than 40% basal skull length (0); more than 40% (1). (C48)

200. Paroccipital process: deep (height ≥ 1/2 length (0); significantly narrower (1). (You & Dodson 2004: 73; Makovicky & Norell 2006: 64; Sereno 2000: 61)

201. Paroccipiatl process, dorsoventral distal expansion: distal process only slightly expanded (0); distal process expanded to at least .8 two times the depth at its narrowest point (1). (Sampson et al. 2010: 108, Forest 1990; 66)

202. Supraoccipital, contribution to foramen magnum: present (0); absent,

eliminated from margin by exoccipital-exoccipital contact on midline (1). (You & Dodson 2004: 74; Makovicky & Norell 2006: 65; Dodson et al. 2004:54; Chinney & Horner 2007: 41; Sampson et al. 2010: 105; Farke et al. 2011: 69)

203. Supraoccipital, ventrolateral processes: absent (0); present (1). (Sampson et al. 2010: 106)

204. Supraoccipital, inclination: incline rostrally relative to basioccipital (0); in the same plane as posterior face of basioccipital (1). (You & Dodson 2004: 75; Makovicky & Norell 2006: 66; Chinney & Horner 2007: 104)

205. Supraoccipital, shape: tall, triangular (0); wider than tall, trapezoid (1); square (2). (You & Dodson 2004: 76; Makovicky & Norell 2006: 67; Chinney & Horner 2007: 42; Xu et al. 2002: 16)

206. Lower jaw, level of articulation with quadrate: same as occlusal surface of tooth row (0); substantially ventral to tooth row (1). (Dodson et al. 2004:56; Chinney & Horner 2007: 67; Sampson et al. 2010: 112)

207. Occipital condyle, size: large (0); small (1). (You & Dodson 2004: 77; Sereno 2000: 62)

208. Predentary length/dentary length: less than two-thirds (0); equal or more than two-thirds (1). (You & Dodson 2004: 78; Makovicky & Norell 2006: 70; C58; Sampson et al. 2010: 113)

209. Predentary, orientation of triturating surface: nearly horizontal (0); inclined steeply laterally (1). (Dodson et al. 2004:57; Sampson et al. 2010: 115; Farke et al. 2011: 57)

210. Tip of predentary, sharp: shallow (0); scooplike (1). (Makovicky & Norell 2006: 68; Xu et al. 2002: 120; Chinney & Horner 2007: 105)

211. Predentary with rounded anterior margin and distally broad posteroventral process (0); with pointed anterior margin and distally narrow posteroventral process (1) (Makovicky & Norell 2006: 69; Xu et al. 2002: 113)

212. Predentary buccal margin: sharp (0); with a rounded, beveled edge (1); with grooved, triturating edge (2). (You & Dodson 2004: 79; Makovicky & Norell 2006: 71; Sereno 2000: 26; Chinney & Horner 2007: 60)

213. Predentary dorsal margin, inclination: horizontal (0); rostrodorsally inclined (1). (You & Dodson 2004: 80; Sereno 2000: 63)

214. Predentary anterior margin: round (0); keeled with point (1). (You & Dodson 2004: 81; Sereno 2000: 13)

215. Predentary surface between dentaries: absent (0); present (1). (You & Dodson 2004: 82; Sereno 2000: 36)

216. Predentary ventral process width of base/maximum transverse width of predentary: less than half (0); equal or more than half (1). (You & Dodson 2004: 83; Sereno 2000: 7)

217. Predentary posteroventral process, shape: broader distally (0); narrower distall (1). (You & Dodson 2004: 84; Sereno 2000: 14)

218. Tip of dentary smooth (0); grooved dorsally for reception of the lateral process of the predentary (1) or bears large pit for reception of the lateral process of the predentary (2). (Makovicky & Norell 2006: 72)

219. Dentary, large pit at anterior end: absent (0); present (1). (You & Dodson 2004: 85; Makovicky & Norell 2006: 54; Chinney & Horner 2007: 63)

220. Dentary ramus, position of maximum dorsoventral width: posterior (0); anterior (1). (You & Dodson 2004: 86; Sereno 2000: 66)

221. Dentary, sharp of ventral margin in adults: strongly convexly bowed (0); straight (1). (You & Dodson 2004: 87; Sereno 2000: 47; Makovicky & Norell 2006: 75; Sampson et al. 2010: 117)

222. Dentary symphyseal area small (0); large, forming strong immobile bond with partici- pation of splenial (1). (Makovicky & Norell 2006: 73)

223. Dentary-prearticular contact: absent (0); present (1). (You & Dodson 2004: 88; Makovicky & Norell 2006: 79; Chinney & Horner 2007: 66)

224. Dentary coronoid process, width and depth: narrow dentary process, low coronoid process (0); broad dentary process, moderately deep coronoid process (1); broad dentary process with distal expansion, very deep coronoid process (2). (You & Dodson 2004: 89; Sereno 2000: 27)

225. Diastema between predentary and first dentary tooth absent (0); present (1). (Makovicky & Norell 2006: 74; Chinney & Horner 2007: 61)

226. Dentary flange, prominence: rugosity (0); low crest (1); prominent flange with anterior corner (2). (After Makovicky & Norell 2006: 76; Xu et al. 2006: 27)

227. Dentary, caudal extent of tooth row: terminates medial to the coronoid process (0); terminates posterior to the coronoid process (1). (Dodson et al. 2004:58; Sampson et al. 2010: 118; Farke et al. 2011: 73)

228. Dentary, shape of the coronoid process: low, with gently convex apex and no neck (0); high, expanded into a rostrally projecting hook at apex, constricted neck present (1). (Dodson et al. 2004:59; Chinney & Horner 2007: 64; Sampson et al. 2010: 119)

229. Prominent medial expansion of the central mandible in the middle of the tooth row formed by wide Meckelian groove separating tooth-bearing part of the jaw from external surface absent (0); present (1). (Makovicky & Norell 2006: 77; Xu et al. 2002: 28)

230. Labial face of dentary smooth below tooth row (0); rugose and sculpted (1). (Makovicky & Norell 2006: 78)

231. Coronoid, shape: strap-shaped (0); lobe-shaped (1). (Sereno 2000: 37; Makovicky & Norell 2006: 83)

232. Distal end of coronoid process: rounded (0); with anterior expansion (1). (You & Dodson 2004: 90; Makovicky & Norell 2006: 81)

233. Angular ventral margin, form: anterior portion convex (0); nearly all of ventral margin convex (1). (You & Dodson 2004: 91; Sereno 2000: 48)

234. Shape of lateral surface of angular: flat or slightly convex (0); angular has a ridge along the ventral margin and the lateral surface is concave (1). (Chinney & Horner 2007: 117)

235. Distinct lateral ridge or shelf overhanging angular: absent (0); present (1). (You & Dodson 2004: 92)

236. Surangular eminence: absent (0); present (1). (You & Dodson 2004: 93; Sereno 2000: 38)

237. Surangular without distinct lateral ridge or shelf overhanging angular (0); shelf/ridge present (1). This probably served for insertion of jaw adductor musculature. (Makovicky & Norell 2006: 84)

238. Surangular, lateral surface: flat or only weakly convex (0); with pronounced later- ally convex curvature (in the transverse plane) between the coronoid process and glenoid region (1). (Makovicky & Norell 2006: 85; Xu et al. 2002: 32; Chinney & Horner 2007: 107)

239. Tab on surangular forming lateral wall to glenoid cotyle: absent (0); present (1). (Makovicky & Norell 2006: 86; Xu et al. 2002: 119; Chinney & Horner 2007: 108)

240. Angular without one or more small, lateral tubercles along ventral rim below glenoid articulation (0); tubercles present (1). (Makovicky & Norell 2006: 87)

241. Lateral surface of angular flat or slightly convex (0); angular bears a raised emargination along posteroventral margin of mandible, lateral surface distinctly concave (1). (Makovicky & Norell 2006: 88)

242. Angular-surangular-dentary contact: triradiate (0); surangular with a long ventral process overlapping angular, and dentary-surangular and angular-surangular sutures form acute angle on lateral face of mandible (1). (You & Dodson 2004: 94; Makovicky & Norell 2006: 89; Chinney & Horner 2007: 68)

243. Mandibular glenoid narrow and flush with medial margin of surangular flange in dorsal view (0); glenoid region medially expanded and forming lingual process in dorsal view (1). (Makovicky & Norell 2006: 90)

244. Surface of prearticular and articular below glenoid smooth (0); with wide, semicircular ventral process near medial face of glenoid (1). (Makovicky & Norell 2006: 91)

245. Retroarticular process length: long, exceeding the length of the glenoid (0); very short or absent (1). (Y95; S15; M92; X29)

246. Splenial symphysis: absent (0); present (1). (You & Dodson 2004: 96; Sereno 2000: 39)

247. Splenial, posterior end: simple or with shallow dent (0); with bifid overlap of angular (1). (You & Dodson 2004: 97; Makovicky & Norell 2006: 80; Chinney & Horner 2007: 116)

248. Premaxillary teeth: present (0); absent (1). (You & Dodson 2004: 98; Sereno 2000: 46)

249. Premaxillary tooth number: 3 or more (0); 1-2 (1); absent (2). (You & Dodson 2004: 99; Sereno 2000: 8; Makovicky & Norell 2006: 93; Chinney & Horner 2007: 71; Xu et al. 2002: 18)

250. Premaxillary teeth with carinae, and in some cases serrations (0); premaxillary teeth peglike, crown without carinae (1). (Makovicky & Norell 2006: 94)

251. Check teeth: spaced (0); loosely oppressed with determinate eruption and replacement pattern (1). (You & Dodson 2004: 101; Makovicky & Norell 2006: 96; Sereno 2000: 19; Chinney & Horner 2007: 73; Sampson et al. 2010: 126)

252. Pronounced cingula on cheek teeth absent (0); present (1). (Makovicky & Norell 2006: 100; Xu et al. 2002: 118)

253. Teeth occlusion: at an oblique angle (0); at a vertical angle (1); at a vertical angle but dentary teeth have a horizontal shelf on the labial face (2). (You & Dodson 2004: 102; Makovicky & Norell 2006: 97; Sereno 2000: 70; Chinney & Horner 2007: 75)

254. Tooth crown, shape: radiate or pennate in lateral view (0); maxillary crowns ovate in lateral view (1). (You & Dodson 2004: 103; Makovicky & Norell 2006: 106; Sereno 2000: 28)

255. Cheek teeth, root-crown connection: cheek teeth cylindrical roots (0); roots with anterior and posterior grooves along root (1). (You & Dodson 2004: 104; Makovicky & Norell 2006: 105; partial Sereno 2000: 29; Chinney & Horner 2007: 78)

256. Dentary tooth, crown: with continuous, smooth root-crown transition (0); bulbous expansion at root-crown transition on labial side of tooth (1). (You & Dodson 2004: 105; Makovicky & Norell 2006: 103; partial Sereno 2000: 29; Chinney & Horner 2007: 79)

257. Base of primary ridge on maxillary teeth: confluent with the cingulum (0); set back from cingulum, which forms a continuous ridge at the crown base (1). (You & Dodson 2004: 106; Makovicky & Norell 2006: 99; Chinney & Horner 2007: 109)

258. Maxillary/dentary teeth, enamel distribution: both sides of crowns (0); restrict to lateral/medial sides in M/D teeth, respectively (1). (You & Dodson 2004: 107; Makovicky & Norell 2006: 102; Sereno 2000: 49; Chinney & Horner 2007: 77)

259. Teeth median primary ridge: absent (0); only on maxillary teeth (1); on both maxillary and dentary teeth (2). (You & Dodson 2004: 108; Makovicky & Norell 2006: 98; Chinney & Horner 2007: 74)

260. Maxillary/dentary teeth, primary ridge, position: near midline (0); offset, posteriorly and rostrally, respectively (1). (You & Dodson 2004: 109; Sereno 2000: 18)

261. Maxillary teeth, primary ridge, development: low (0); prominent (1). (You & Dodson 2004: 110; Sereno 2000: 17; Xu et al. 2002: 19)

262. Dentary teeth, primary ridge, development: low (0); prominent (1). (You & Dodson 2004: 111; Sereno 2000: 64)

263. Maxillary (lateral view)/ dentary (medial view) crowns, secondary ridge: present (0); rudimentary or absent (1). (You & Dodson 2004: 112; Sereno 2000: 71)

264. Maxillary crowns, maximum width relative to height: 75% (0); subequal (1). (Sereno 2010)

265. Teeth, number of roots: one (0); two (1). (You & Dodson 2004: 113; Sereno 2000: 69; Makovicky & Norell 2006: 95; Dodson et al. 2004:60; Chinney & Horner 2007: 72; Sampson et al. 2010: 123; Farke et al. 2011: 74)

266. Tooth, number of replacements per alveolus: one or two replacement teeth (0); three or more replacement teeth (1). (You & Dodson 2004: 114; Makovicky & Norell 2006: 101; Chinney & Horner 2007: 76; Dodson et al. 2004:61; Sampson et al. 2010: 124; Farke et al. 2011: 76)

267. Number of alveoli in dentary: less than 20 (0); more than 20 (1). (You & Dodson 2004: 115; Makovicky & Norell 2006: 104; Chinney & Horner 2007: 80; Farke et al. 2011: 75)

268. Dentary tooth row, position of last tooth, relative to apex of coronoid process: anterior to (0); coincident with (1); posterior to (2). (You & Dodson 2004: 116; Sereno 2000: 20; Makovicky & Norell 2006: 82)

269. Tooth ornamentation: subsidiary ridges present, extend from margin to base of tooth (0); subsidiary ridges reduced, present only at margin of teeth (1). (Dodson et al. 2004:62)

270. Hypocentrum shape: wedge-shaped (0); U-shaped (1); ring-shaped (hemespherical occipital condyle) (2); absent (3). (You & Dodson 2004: 117, 118; Sereno 2000: 56, 67)

271. Atlas intercentrum: semicircular (0); disc/ring-shaped (1). (You & Dodson 2004: 119; Makovicky & Norell 2006: 107; Chinney & Horner 2007: 82)

272. Atlas intercentrum: not fused to odontoid (0); fused to odontoid (1). (You & Dodson 2004: 120; Makovicky & Norell 2006: 108; Chinney & Horner 2007: 118)

273. Atlas neuropophyses: free (0); fused to intercentrum/odontoid (1). (You & Dodson 2004: 121; Makovicky & Norell 2006: 109; Chinney & Horner 2007: 119)

274. Axial neural spine: low (0); tall and hatchet-shaped (1); elongate and posteriorly inclined (2). (You & Dodson 2004: 122; Makovicky & Norell 2006: 110; Sereno 2000: 40; Chinney & Horner 2007: 83)

275. Atlas, neural arch orientation: nearly vertical (0); steeply inclined posteriorly (1). (Dodson et al. 2004:63)

276. The neural spine of the axis anteroposteriorly short (0); long, extending posteriorly to the posterior end of the centrum of the succeeding cervical (1). (Makovicky & Norell 2006: 111; Xu et al. 2002: 112)

277. Syncervicle: absent (0); partially fused (centra but not arches) (1); completely coossified (2). (You & Dodson 2004: 123; Makovicky & Norell 2006: 112; Sereno 2000: 41; Chinney & Horner 2007: 81)

278. Cervicals 3-4, neural spine height, compared to spine height of axis: much shorter (0); subequal (1). (You & Dodson 2004: 124; Sereno 2000: 42)

279. Mid cervicals (C5-C7) neural spines, height: low (0); as high as dorsal neural spines (1). (You & Dodson 2004: 125; Sereno 2000: 68)

280. Dorsal vertebrae: with flat articular zygapophyseal (0); tongue and groove articulations on zygapophyses (1). (You & Dodson 2004: 126; Makovicky & Norell 2006: 113; Chinney & Horner 2007: 110)

281. Outline of sacral: rectangle or hourglass in dorsal view (0); oval in dorsal view (1). (You & Dodson 2004: 127; Makovicky & Norell 2006: 115)

282. Sacral neural spines, mutual contact: absent (0); present (1). (You & Dodson 2004: 128; Sereno 2000: 58)

283. Sacral number: 5 or less (0); 6 (1); more than 6 (2); more than 8 (3). (You & Dodson 2004: 129; Sereno 2000: 57; Makovicky & Norell 2006: 114; Chinney & Horner 2007: 84)

284. Posterior neural spine: short or inclined (0); tall and straight (1). (You & Dodson 2004: 130; Makovicky & Norell 2006: 116; Sereno 2000: 45)

285. Mid and distal posteriors, neural spine cross-section: subrectangular (0); oval (1). (You & Dodson 2004: 131; Sereno 2000: 44)

286. The height ratio of middle caudal neural spine to associated centrum: less than or equal to 2 (0); 2.1 ~ 3 (1); 3.1 ~ 4 (2); more than 4.1 (3). (Lee et al. 2010: 134)

287. The height of the caudal neural spine is greater than the length of the chevron for any given caudal vertebra: absent (0); present (1). (Lee et al. 2010: 136)

288. Distal chevrons: lobate expanded shape (0); rod-like (0). (You & Dodson 2004: 132; Makovicky & Norell 2006: 118)

289. Distalmost posteriors, neural spines and chevrons: absent (0); present (1). (You & Dodson 2004: 133; Sereno 2000: 43; Makovicky & Norell 2006: 117)

290. Clavicles: absent (0); present and robust (1). (You & Dodson 2004: 134; Makovicky & Norell 2006: 119; Chinney & Horner 2007: 86; Sampson et al. 2010: 135; Farke et al. 2011:84)

291. Scapular in lateral view: distinctly curved (0); relatively flat (1). (You & Dodson 2004: 135; Makovicky & Norell 2006: 120; Chinney & Horner 2007: 87)

292. Scapular blade: at acute angle relative to glenoid (0); almost perpendicular to glenoid (1). (You & Dodson 2004: 136; Makovicky & Norell 2006: 121; Chinney & Horner 2007: 88)

293. Coracoid with smooth, arcuate anterior portion (0); bearing large anterolateral ridge near confluence of anterior and ventral margins (1). (Makovicky & Norell 2006: 122)

294. Olecranon process: relatively small (0); enlarged (one-third of ulnar length) (1). (You & Dodson 2004: 137; Makovicky & Norell 2006: 123; Chinney & Horner 2007: 90; Sampson et al. 2010: 134; Farke et al. 2011: 82)

295. Sacrum, number of fused vertebrae: eight or less (0); ten or more (1). (Dodson et al. 2004:64)

296. Sacrum, deep longitudinal channel on ventral surface: present (0); absent (1). (Dodson et al. 2004:65; Sampson et al. 2010: 131)

297. Sacrum, shape in dorsal view: rectangle or hourglass shape (0); oval (1). (Chinney & Horner 2007: 120)

298. Sternum, shape: elongate and narrow (0); short and broad (1). (Dodson et al.

2004:66)

299. Shape of distal ulna: relatively straight shaft (0); pronounced medial bend of distal shaft (1). (Chinney & Horner 2007: 91)

300. Number of distal carpals: more than 2 (0); less than 2 (1). (You & Dodson 2004: 138; Makovicky & Norell 2006: 124; Chinney & Horner 2007: 121)

301. Manus/pes: manus much smaller than pes (0); close to pes in size (1). (You & Dodson 2004: 139; Makovicky & Norell 2006: 125; Chinney & Horner 2007: 122)

302. Pes shape: gracile with constricted metatarsals (0); shorter, more robust, with unconstricted metatarsals (1). (Chinney & Horner 2007: 97)

303. Manus phalange: slender (0); wider than long (1). (You & Dodson 2004: 140)

304. Manual and pedal unguals, shape: clawlike (0); hooflike (1). (Dodson et al. 2004:67; Chinney & Horner 2007: 96; Sampson et al. 2010: 137; Farke et al. 2011: 85)

305. The width of proximal end of the ungula relative to width of distal end of the preceding phalanx: equal (0); wider (1). (Lee et al. 2010: 135)

306. Shaft of postpubis in cross section: round (0); mediolaterally flattened, bladelike (1). (You & Dodson 2004: 141; Makovicky & Norell 2006: 126)

307. Postpubic process: long and ventrally oriented (0); short and posteriorly directed (1). (You & Dodson 2004: 142; Makovicky & Norell 2006: 127; Xu et al. 2002: 47)

308. Prepubic process: short and rod-shaped (0); long and flared at anterior end (1). (You & Dodson 2004: 143; Makovicky & Norell 2006: 128; Chinney & Horner 2007: 92)

309. Ischial shaft: straight (0); curved, posterodorsally convex (1). (You & Dodson 2004: 144; Makovicky & Norell 2006: 129; Chinney & Horner 2007: 93)

310. Femoral fourth trochanter: large and pendant (0); reduced (1). (You & Dodson 2004: 145; Makovicky & Norell 2006: 130; Chinney & Horner 2007: 94; Sampson et al. 2010: 146; Farke et al. 2011: 95)

311. Femur, coalescence of greater and cranial trochanters: absent (0); present (1). (Dodson et al. 2004:72; Sampson et al. 2010: 145; Farke et al. 2011: 94)

312. Femur-tibia proportion: tibia longer than femur (0); femur longer than tibia (1). (You & Dodson 2004: 146; Makovicky & Norell 2006: 131; Dodson et al. 2004:73; Chinney & Horner 2007: 95; Sampson et al. 2010: 147; Farke et al. 2011: 96)

313. Foot: gracile with long, constricted metatarsus, elongate phalanges (0); short and uncompressed, stubby phalanges (1). (You & Dodson 2004: 147; Makovicky & Norell 2006: 132)

314. Pedal unguals: pointed (0); moderately rounded, hooflike (1). (You & Dodson 2004: 148; Makovicky & Norell 2006: 133)

315. Ilium, laterally everted shelf on dorsal margin: absent (0); present (1). (Dodson et al. 2004:68; Sampson et al. 2010: 138; Farke et al. 2011: 87)

316. Ilium, supracetabular process on dorsal margin over posterior part of acetabulum: absent (0); present (1). (Dodson et al. 2004:69)

317. Ischium, cross-sectional shape of shaft: ovoid (0); laterally compressed and bladelike, narrow along dorsal margin (1). (Dodson et al. 2004:70; Sampson et al. 2010: 143; Farke et al. 2011: 92)

318. Ischium, orientation of shaft: nearly straight (0); slightly decurved (1); broadly and continuously curved (2). (Dodson et al. 2004:71; Sampson et al. 2010: 144; Farke et al. 2011: 93)

II. Data Matrix

Pachycephalosauria

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2??0?0??03????????????????????????????????????
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Psittacosaurus_mongoliensis

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Psittacosaurus_neimongoliensis

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Psittacosaurus_sinensis

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Psittacosaurus_lujiatunensis

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Psittacosaurus_major

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Psittacosaurus_sibiricus

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Chaoyangsaurus_youngi

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Liaoceratops_yanzigouensis

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Yamaceratops_dorngobiensis

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Archaeoceratops_oshimai

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Archaeoceratops_yujingziensis

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Helioceratops_brachygnathus

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Graciliceratops_mongoliensis

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Montanoceratops_cerorhynchus

1?1?????1?0?1?2???010?0???????1?????????????????????????????0??????????0???

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??0?0100??1?11???1?110?2?0121111121100?0001?10111??1101012112110110???

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Prenoceratops_pieganensis

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Bainoceratops_efremovi

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Udanoceratopsts_chizhovi

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Leptoceratops_gracilis

10121100100011100001000111 11?01001 1?220202000202?1000000000?01??02?022

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02022302 0??20?0??022?10?0000010101101010 00?111?111??1001?1100010001011

1111112100111000010101101011010101101 2?012111112110 0?0001?00101?11100

0011?0?1101100100?0000100000000000?00

Protoceratops_andrewsi

10141000100012100001011011010?12?10?220????0??0??1000?000000?0??12?0220

0000?01?01?01100111002201011?00???????0?100?0????1?2100000110010000000

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1111110003111000101001111110111011101101011001211 00?0001030111011101 0

12112111011000000000000110000000010000

Protoceratops_hellenikorhinus

1014100010001210000101 1???????12?10???0????0??0??1000?000?00?0??12?02200

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1111001311100010100111111011101110110101100121100?????????????????????

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Bagaceratops_rozhdestvenskyi

1?1310?0101012 1?00111 11?1110?11101????0??????????????????00???10??12??????0

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0111110?0?01?0111111?11101?112?0101100121100?0001???????0?????????31????

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Zuniceratops_christopheri

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1011?0?????1????????????2??1100000021??1???001?????????????0?1????10????????

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Turanoceratops_tardabilis

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Cerasinops_hodgskissi

1012????????1???0????????????????1?????????????????????????????0??02??????0???

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Achelousaurus_horneri

10140110011???1????221?01???0?1????10?0???00??0??110??1?????????20?20?1??

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011??01?111?0????1?111?????????????????????1?????1???1???1??1?????????????

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Avaceratops_lammersi

101?01100?1????????221?11???0?1?????0?0???00??0??00?????????????????????1???

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Centrosaurus_apertus

10140110011100211112211011100010111007?0???01??0??1100?100111?0002??101

101?111211?1111111121121102?1100011211?2110111001?2201100110111101 1

01111112110000121111000111111101111110111011111100211101111001111210011120111110111121011001100000110007010012?1111100121111?1112121112112

11011300001110101111101111111111111111102

Pachyrhinosaurus_canadensis

10140117011107????????1?011100?10????0?0???00??0??110??1??????????20020?1??

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11100??2111?0????1?1110?????????????????????1?????1???1???1??1????????????

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Pachyrhinosaurus_lakustai

10140110011107?2111?221?011100?10????0?0????1??0??1100?1??111???????20?10

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Einiosaurus_procurvicornis

10140110011107??????221001?????10??100?00?0?1100?110??1001101???1???011?

111?1??1???????10021????101211????11???11100110?0110021117011111117?1???

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Styracosaurus_albertensis

10140110017??0?????221?0111000107??00?0???00??0??110??1??????????20010117

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2111000121117?00???1?1110?????????????????????????1?????1???1???1??1???????????

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Albertaceratops_nesmoi

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Diabioceratops_eatoni

10?3001001110001117?221?01?????10????0?0???0???0??1100?1???11?????0000117

1???1?????1??1?11111??1??2??1100000l2???1???000????2111????01111?1101117

1????10001211170O??111?110?????????????????????1????????1?1?????????????????

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Chasmosaurus_russelli

10140110011100111???111111100101??0101010000010000l0?1??111????1??100

011?111?????1??11???21??1??2??11000?1020?2111?????????20011???00111010011

00211000112011007?1???1010011?????????????1????????1???1?1??111??1?00??????

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Chasmosaurus_belli

10140110011100111?221?1111100101??0101010007010000100l??111????100100

011?111?????1??11???21??1??2??11000?1020?2111100l????20011???00111010011

00211000111011007?11??1010011?????????????1????????1???1?1??111??1?00??????

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Mojoceratops_perifania

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Agujaceratops_mariscalensis

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1?1?????1?????111??1112

Utahceratops_gettyi

10140110011101?111?2211111110010????10101100??1100011?1??1111000???10?

001?1112?2101110?11111?????2???1?11?122??2111????????21?11???001?1?10111

??3??????121?????1???1010?11?????????????1?????????????1????1????1?00????????

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Pentaceratops_sternbergii

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001?111?????1??0????1112110207?1100000127?2111100101122101101100111010 11

10031100011211100?1101101001111111101110111111002111011110011112100011201111101111210110011000001100010100127?111100121111?1112121112112110113000011101011111011111111111111111112

Coahuilaceratops_magnacuerna

1014?????????????1??????1?????????????1011??00?0???0??1?1??111????1001100?????????????????2???????????2???10???01?????????????????????11???001?1??0???????????1?1??1???1???1??0?1?????????????????????????????????????0????????????1?????11?????????????????????1???

Kosmoceratops_richardsoni

10140110011107111?221?11?????10????10111100?1100010?1??111???????10?001?111?????1??0????11?????2???1?01?012??2111????????21?11???001?0?10011??2??????011?????1???1000?10?????????????????????????????????1?00???????????1??????1?????????????????????1?????????????1?????????????????????1???????????????????

Vagaceratops_irvinensis

10140110011100111?2211111?????10????10111000007?00010?1??111???????1000001?111?????1??11???21??1??2???10????0?0?21?11???????2101 1???001100?001000211000111??1100?1???1000011?????????????????????1???1?1??111??1?00?????????1?????11?????????????????????1?????????????11??1?????1?????????????1????11?1?????1?????111??1112

Anchiceratops_ornatus

10140110011107211?221?11?????10????10110?0000110010071??111????1001100001?111?????1??02???11??1??2???1011?011??2112100 0????2101 1???001100110100

0?0100000?21100?1???1010011?????????????1????????1???1?1??111??1??0????????

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Arrhinoceratops_brachyops

10140110011?0?2111?221?11??00010????10110?000?1?00100?1??11?????1001100

01?111?????1??0????21??1??2??11011?011???112?000????2101???001100110100

040?00000?21????1???10?0011?????????????1????????1???1?1??111??1???????????

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Torosaurus_latus

10140110011110?2111?221??1?1?0?10???110100?1011???010??1??111????1101100

01?111?????1??02???21??1??2???1010?0120?21?21000????22011???001101110100

040000000?01100?1???1010011?????????????1????????1???1?1??111??1??0????????

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Torosaurus_utahensis

10140110011100?111?221?11?1?0?10???110100?1011???010?????????????11011000

1?111?????1??0????2??????2??11?10?012??2???????????22?11???001?0?110?0??4?

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Nedoceratops_hatcheri

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1?111????????02???2???1??????1010?012??2112????????12011????011011101?00?

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Triceratops_horridus

10140110011100211112211111110010101110100?101111101001100111100011111
0001?1112?1101110211121121102 2?1101000120?2112100001121211101110010 01
1?1000400000???0111011101101001111111101110111111002111011110011112 10
00112011111011112101100110000011000101001 2?1111100121111?111212111211
211011300001110101111101111111111111111112

Triceratops_prorsus

10140110011100211 1?221?11???0?10???110100?101?1110100?1??1111000???11?0
01?111?????1???????21?????2??11?10?012????12????????12?11???100???1??10??4
????????0?????1???1010?11?????????????1?????????????1????111??1?00????????????
1?????11?????????????????????????????????????11?????????????????????????????
??????????????????? A list of ingroup terminals

III. A list of ingroup terminals

Taxa	Geological formation	Stratigraphic stage
Yinlong downsi	Shishugou Formation	Oxfordian
Psittacosaurus meileyingensis	Jiufotang Formation	Aptian
Psittacosaurus mongoliensis	Khukhtekskaya Svita	late Aptian–Albian

	unnamed unit	Aptian–Albian
	Khulsyngolskaya Svita	Aptian
	Shinekhudag Svita	Aptian
	Khukhtekskaya Svita	late Aptian–Albian
	Jiufotang Formation	Albian
	unnamed unit	Aptian–Albian
	Shestakovskaya Svita	Aptian–Albian
Psittacosaurus neimongoliensis	Ejinhoro Formation	early Aptian
Psittacosaurus osborni	Lisangou Formation	early Aptian
	Xinpongnaobao Formation	early Aptian
Psittacosaurus sinensis	Doushan Formation	late Aptian
Psittacosaurus xinjiangensis	Lianmuqin Formation	early Aptian
	Shestakovskaya Svita	
Psittacosaurus lujiatunensis	Yixian Formation	Barremain
Psittacosaurus major	Yixian Formation	Barremain

Psittacosaurus gobiensis	Bayan Gobi Formation	Aptian
Psittacosaurus sibiricus	Ilek Formation	late Aptian–Albian
Archaeoceratops oshimai	Xinminpu Group	Albian
Archaeoceratops yujingziensis	Xinminpu Group	?Aptian-Albian
Archaeoceratops rozhdestvenskyi	Red Beds of Hermiin Tsav Baruungoyot Formation	middle Campanian
Archaeoceratops niei	Houcheng Formation	?Late Jurassic
Archaeoceratops youngi	Tuchengzi Formation	Tithonian
Graciliceratops mongoliensis	Shireegiin Gashuun Formation	Cenomanian–Santonian
Liaoceratops yanzigouensis	Yixian Formation	Barremain
Leptoceratops gracilis	Scollard Formation	late Maastrichtian
	Lance Formation	late Maastrichtian
	Hell Creek Formation	late Maastrichtian

Zhuchengceratops inexpectus	Wangshi Group	Upper Cretaceous
Ajkaceratops kozmai	Csehbánya Formation	Santonian
Montanoceratops cerorhynchus	St. Mary River Formation	early Maastrichtian
	Horseshoe Canyon Formation	early Maastrichtian
Protoceratops andrewsi	Djadokhta Formation	late Santonian or early Campanian
	Minhe Formation	late Santonian or early Campanian
	Djadokhta Formation	late Santonian or early Campanian
	Minhe Formation	late Santonian or early Campanian
Protoceratops hellenikorhinus	Djadokhta Formation	?late Santonian or early Campanian
Udanoceratops tschizhovi	Djadokhta Formation	?late Santonian or early Campanian
Zuniceratops christopheri	Moreno Hill Formation	Turonian

Turanoceratops		
tardabilis	Bissekty	Turonian
Auroraceratops		
rugosus	Xinminpu Group	early Albian
Helioceratops		
brachygnathus	Quantou Formation	Albian
Yamaceratops		
dorngobiensis	Khar Khutul bed	Barremain
Gobiceratops minutus	Baruungoyot Formation	Upper Cretaceous
Bainoceratops		
efremovi	Djadokhta Formation	late Campanian
Cerasinops hodgskissi	Two Medicine River Formation	late Campanian
Prenoceratops		
pieganensis	Two Medicine River Formation	late Campanian
Lamaceratops		
tereschenkoi	Barun Goyot Formation	Late Santonian
Platyceratops		
tatarinovi	Barun Goyot Formation	Late Santonian
Achelousaurus horneri	Upper Two Medicine Formation	late Campanian
Avaceratops lammersi	Judith River Formation	late Campanian

Centrosaurus apertus	Dinosaur Park Formation	late Campanian
Einiosaurus procurvicornis	Two Medicine Formation	late Campanian
Rubeosaurus ovatus	Two Medicine Formation	late Campanian
Pachyrhinosaurus canadensis	Horseshoe Canyon Formation	Maastrichtian
	St. Mary River Formation	Maastrichtian
	Prince Creek Formation	Maastrichtian
Pachyrhinosaurus lakustai	Upper Bearpaw Formation	Maastrichtian
	Lower Horseshoe Canyon Formation	Maastrichtian
Styracosaurus albertensis	Dinosaur Park Formation	late Campanian
Albertaceratops nesmoi	Oldman Formation	middle Campanian
Diabloceratops eatoni	Wahweap Formation	early - middle Campanian
Sinoceratops zhuchengensis	Wangshi Group	Upper Cretaceous

Brachyceratops		
montanensis	Upper Two Medicine Formation	late Campanian
Monoclonius crassus	Judith River Formation	late Campanian
	Dinosaur Park Formation	late Campanian
Anchiceratops ornatus	Dinosaur Park Formation	late Campanian–Maastrichtian
	Horseshoe Canyon Formation	late Campanian–Maastrichtian
Arrhinoceratops		
brachyops	Horseshoe Canyon Formation	Maastrichtian
Coahuilaceratops		
magnacuerna	Cerro del Pueblo Formation	middle Campanian
Chasmosaurus belli	Dinosaur Park Formation	late Campanian
Chasmosaurus russelli	Dinosaur Park Formation	late Campanian
Mojoceratops perifania	Dinosaur Park Formation	late Campanian
Agujaceratops		
mariscalensis	Aguja Formation	Campanian
Kosmoceratops		
richardsoni	Kaiparowits Formation	late Campanian

Vagaceratops irvinensis	Dinosaur Park Formation	late Campanian
Nedoceratops hatcheri	Lance Formation	Maastrichtian
Utahceratops gettyi	Kaiparowits	late Campanian
Pentaceratops sternbergii	Fruitland Formation	?Campanian-Maastrichtian
Torosaurus latus	Lance Formation	late Maastrichtian
	Hell Creek Formation	late Maastrichtian
	Hell Creek Formation	late Maastrichtian
	Hell Creek Formation	late Maastrichtian
	Laramie Formation	late Maastrichtian
	North Horn Formation	late Maastrichtian
	Upper Kirtland Formation	late Maastrichtian
	McCrae Formation	late Maastrichtian
	Javelina Formation	late Maastrichtian
Torosaurus utahensis	Hell Creek Formation	late Maastrichtian
Torosaurus horridus	Lance Formation	late Maastrichtian
	Evanston Formation	late Maastrichtian

	Hell Creek Formation	late Maastrichtian
	Hell Creek Formation	late Maastrichtian
	Hell Creek Formation	late Maastrichtian
	Laramie Formation	late Maastrichtian
	Scollard Formation	late Maastrichtian
	Frenchman Formation	late Maastrichtian
Torosaurus. prorsus	Hell Creek Formation	late Maastrichtian
Eotriceratops xerinsularis	Horseshoe Canyon Formation	late Maastrichtian
Ojoceratops fowleri	Ojo Alamo Formation	late Maastrichtian
Medusaceratops lokii	Judith River Formation	late Maastrichtian
Tatankaceratops sacrisonorum	Hell Creek Formation	late Maastrichtian

IV. Ceratopsian TDE data for analysis

	Duration	Ceratopsian TDE	Ceratopsian TDE with mid-age	Ceratopsian TDE with ghost lineage	Ceratopsian TDE in each Ma	Ceratopsian TDE with mid-age in each Ma	Ceratopsian TDE with ghost lineage in each Ma
Oxf-l	1.7	1	1	1	0.59	0.59	0.59
Oxfm	2.1	1	1	6	0.48	0.48	2.86
Oxf-u	2.8	1	0	3	0.36	0.00	1.07
Kim	3.8	1	0	5	0.26	0.00	1.32
Tth-l	3.6	2	1	4	0.56	0.28	1.11
Tth-u	1.7	2	0	5	1.18	0.00	2.94
Ber-l	3.1	3	0	6	0.97	0.00	1.94
Ber-u	2.2	3	0	7	1.36	0.00	3.18
Vlg-l	1.2	3	0	7	2.50	0.00	5.83
Vlg-u	2.6	3	0	7	1.15	0.00	2.69
Hau-l	2.5	3	0	13	1.20	0.00	5.20

Hauu	3.9	3	0	10	0.77	0.00	2.56
Brm-l	1.7	7	0	12	4.12	0.00	7.06
Brmu	3.3	7	4	12	2.12	1.21	3.64
Apt-l	4	10	2	8	2.50	0.50	2.00
Aptm	6	6	1	10	1.00	0.17	1.67
Apt-u	3	9	2	9	3.00	0.67	3.00
Alb-l	3.2	11	2	6	3.44	0.63	1.88
Albm	2.4	8	1	6	3.33	0.42	2.50
Alb-u	6.8	8	3	6	1.18	0.44	0.88
Cen-l	3.4	2	0	2	0.59	0.00	0.59
Cenm	1.1	2	0	3	1.82	0.00	2.73
Cenu	1.6	2	0	4	1.25	0.00	2.50
Tur	4.2	3	3	13	0.71	0.71	3.10
Con	3.5	2	0	20	0.57	0.00	5.71
San	2.3	8	4	19	3.48	1.74	8.26
Cmpl	2.9	7	1	20	2.41	0.34	6.90

Cmpm	4.2	7	5	28	1.67	1.19	6.67
Cmp u	5.8	22	18	32	3.79	3.10	5.52
Maa-l	1.3	7	1	10	5.38	0.77	7.69
Maa-u	3.8	12	12	13	3.16	3.16	3.42

V. Scores of all species in all axes.

Pachycephalosauria	0	16.451317	17.916473	15.434588	16.419116
	16.534686	17.916473	17.916473	17.916473	17.916473
	17.916473	15.697958	15.788451	16.321389	16.649538
	13.983387	16.266127	14.958275	16.080355	15.161055
	17.916473	16.649538	16.720237	17.916473	17.076373
	16.246075	17.344512	17.420922	17.133064	15.468203
	14.361058	16.90306	15.312495	13.520817	16.333341
	17.916473	15.041609	14.499655	14.966312	15.312495
	14.615014	14.322731	17.916473	14.134201	14.134201
	14.640617	14.737483	14.421815	16.199249	17.916473
	12.829204	13.558219	14.527216	14.499655	13.990738
	16.152709	14.723626	14.101484	14.966312	16.312277
	14.243688	15.215805			
Yinlongdownsi	16.451317	0	13.520817	14.191251	11.793504
	13.631306	12.45633	14.160703	12.624975	12.624975
	17.916473	10.404081	9.9766	9.748846	8.566833	7.658057
	9.205976	8.9861	10.860939	17.916473	9.013878	7.898592
	7.898592	17.916473	7.658057	10.509202	9.367497	
	8.955356	10.335647	13.990738	0	10.064606	15.215805
	15.384859	12.220202	14.958275	13.865371	12.908627	
	13.548524	14.160703	14.388885	14.838228	17.916473	
	15.981471	16.180544	17.916473	15.953637	15.864369	
	13.785774	15.953637	16.566166	16.749925	15.864369	

	15.732629	17.916473	17.916473	15.864369	16.824577
	16.664609	13.422693	15.583324	15.704796	
Psittacosaurusmeileyingensis	17.916473	13.520817	0	10.306618	
	9.942747	9.734996	9.718862	9.077479	9.027658
	8.975146	17.916473	13.990738	16.080355	13.113617
	13.603768	12.027746	14.101484	17.916473	14.388885
	17.916473	17.916473	13.865371	16.315586	17.916473
	15.953637	15.556464	16.266127	16.080355	15.373404
	17.916473	17.916473	13.113617	16.890447	16.451317
	15.566985	17.916473	16.749925	15.981471	14.737483
	15.013882	15.953637	16.824577	17.916473	16.265861
	16.343422	15.704796	14.388885	15.66304	16.266127
	14.361058	16.824577	16.086246	15.981471	15.864369
	17.916473	17.916473	15.440472	15.013882	15.215805
	15.096909	13.782946	14.388885		
Psittacosaurusmongoliensis	15.434588	14.191251	10.306618	0	
	11.932169	13.333777	11.181381	11.147809	9.5 9.027658
	17.916473	14.610957	14.612226	14.92222	14.992687
	13.732126	13.986362	15.013882	15.049718	14.855984
	15.732629	16.108593	15.205482	15.171047	15.404949
	15.75988	16.386446	16.043768	15.288317	15.064617
	17.916473	14.664242	16.510896	15.788148	16.375853
	17.916473	16.510896	16.26104	15.166761	16.119921
	16.464284	16.778408	17.916473	16.133768	16.333341
	16.146549	15.984947	15.704667	16.28506	16.180544

15.551101 16.071543 16.368779 15.910356 15.215805

17.916473 15.998893 15.38173 15.744285 16.138566

14.822323 14.444376

Psittacosaurusneimongoliensis 16.419116 11.793504 9.942747

11.932169 0 10.190807 10.139012 10.125402 8.654623

9.027658 17.916473 13.422693 14.990079 14.527216

13.502783 10.593601 13.03652 11.97219 16.594003

17.916473 13.113617 14.366107 14.134201 17.916473

14.243688 14.728411 15.716437 15.804657 14.745847

15.788148 16.152709 13.948341 15.212955 16.208331

14.552194 15.171047 15.003806 14.81245 14.031735

14.63694 16.419116 15.003806 15.704796 15.862103

15.926099 17.003738 16.019439 15.17627 15.529992

16.343422 16.054763 16.020378 15.863052 15.286142

17.916473 17.304484 15.041592 14.430165 15.483829

14.633711 14.121261 14.160436

Psittacosaurussinensis 16.534686 13.631306 9.734996 13.333777

10.190807 0 10.29588 10.468314 8.654623 8.581328

17.916473 13.849639 15.152939 15.038711 14.185698

13.413082 14.01249 14.986105 15.639865 16.948998

13.113617 15.140947 14.382641 15.953637 14.762697

15.052467 16.090078 15.936039 15.306866 14.366107

17.916473 14.894766 16.208331 16.180544 15.598 17.916473

16.266127 15.972089 15.103921 15.340758 16.538875

16.419116 17.916473 15.651481 15.651481 17.001385

	15.556464	14.935398	15.589367	15.41269	16.506943
	16.361073	16.689023	16.036994	15.953637	17.916473
	15.639865	14.462834	16.320311	15.075479	14.120863
	14.640617				
Psittacosauruslujiatunensis	17.916473	12.45633	9.718862	11.181381	
	10.139012	10.29588	0	9.952688	9.269896	8.581328
	17.916473	14.416657	16.141771	16.152709	13.785774
	14.714641	15.011587	17.916473	16.749925	17.916473
	17.916473	14.838228	15.732629	17.916473	16.566166
	15.051646	16.19013	16.464284	16.320311	17.916473
	17.916473	15.215805	17.916473	17.916473	15.69416
	17.916473	17.916473	17.16538	15.856015	16.479153
	16.749925	17.197838	17.916473	17.366407	17.401434
	16.664609	15.013882	16.320311	16.19013	17.916473
	17.916473	17.326548	17.304484	17.16538	17.916473
	17.916473	16.777763	16.538875	17.129972	15.69416
	15.788148	16.566166			
Psittacosaurusmajor	17.916473	14.160703	9.077479	11.147809	
	10.125402	10.468314	9.952688	0	9.077479	9.027658
	17.916473	13.865371	16.852415	14.388885	14.472042
	13.520817	14.615253	17.916473	15.583324	17.916473
	17.916473	14.640617	16.451317	17.916473	16.315586
	16.37121	16.918285	16.816293	16.080355	17.916473
	17.916473	14.986105	17.129972	16.664609	15.326621
	17.916473	17.048534	16.180544	15.373404	15.556814

16.566166 17.048534 17.916473 16.594003 16.645048

15.953637 14.416657 15.271314 16.320311 15.384859

16.948998 16.414238 16.414238 16.086246 17.916473

17.916473 15.849997 15.312495 16.824577 15.254081

14.737483 15.215805

Psittacosaurusgobiensis 17.916473 12.624975 9.027658 9.5

8.654623 8.654623 9.269896 9.077479 0 8.502723

17.916473 12.027746 16.645048 13.990738 13.576174

10.321367 13.603768 17.916473 14.986105 17.916473

17.916473 13.520817 15.953637 17.916473 15.953637

15.932689 16.645048 16.479153 15.66304 15.953637

17.916473 13.990738 17.001385 16.566166 14.615253

17.916473 16.890447 15.981471 14.472042 15.171047

16.152709 15.864369 17.916473 15.556814 15.66304

15.704796 14.714641 15.66304 15.373404 14.361058

16.824577 16.180544 16.086246 15.013882 17.916473

17.916473 15.556814 14.04622 16.566166 14.723626

13.782946 13.113617

Psittacosaurussibiricus 17.916473 12.624975 8.975146 9.027658

9.027658 8.581328 8.581328 9.027658 8.502723 0

17.916473 13.493054 16.594003 15.384859 13.078467

12.853174 14.160436 17.916473 16.152709 17.916473

17.916473 13.990738 15.953637 17.916473 17.916473

16.479153 17.227699 17.129972 16.265861 17.916473

17.916473 14.958275 17.916473 17.916473 15.468203

	17.916473	17.916473	16.824577	15.440472	15.732629
	16.152709	16.749925	17.916473	16.948998	17.001385
	15.704796	14.714641	16.265861	15.932689	17.916473
	17.916473	16.948998	16.890447	16.749925	17.916473
	17.916473	16.086246	15.41269	16.566166	15.556464
	14.615014	15.704796			
Koreaceratopshwaseongensis	17.916473	17.916473	17.916473	17.916473	
	17.916473	17.916473	17.916473	17.916473	17.916473
	17.916473	0	17.916473	17.916473	11.97219
	17.916473	17.916473	17.916473	13.465233	17.916473
	17.916473	12.027746	11.97219	7.249828	10.805554
	13.493054	12.027746	17.916473	6.027714	17.916473
	17.916473	17.916473	17.916473	17.916473	15.953637
	17.916473	17.916473	17.916473	11.97219	17.916473
	17.916473	17.916473	17.916473	17.916473	17.916473
	17.916473	17.916473	17.916473	15.704796	17.916473
	17.916473	17.916473	17.916473	17.916473	17.916473
	17.916473	17.916473	17.916473	17.916473	15.704796
	17.916473	17.916473			
Chaoyangsaurusyoungi	15.697958	10.404081	13.990738	14.610957	
	13.422693	13.849639	14.416657	13.865371	12.027746
	13.493054	17.916473	0	14.317813	15.123133
	14.14639				
	13.741065	12.451129	14.838228	13.514281	17.091192
	10.589893	14.993579	15.003806	17.916473	14.211367
	15.575856	15.27406	14.375438	14.817207	15.760413

	17.916473	13.929944	14.714641	13.990738	15.910905
	17.916473	15.732629	15.312495	15.556814	15.583324
	15.953637	16.451317	17.916473	15.66304	15.66304
	17.916473	16.566166	15.373404	16.344244	12.027746
	14.640617	15.013882	15.732629	15.583324	14.958275
	17.916473	15.732629	14.838228	17.916473	15.953546
	14.838228	12			
Liaoceratopsyanzigouensis	15.788451	9.9766	16.080355	14.612226	
	14.990079	15.152939	16.141771	16.852415	16.645048
	16.594003	17.916473	14.317813	0	11.677738 12.083693
	11.901018	13.613786	13.865371	12.600423	15.271314
	6.137318	12.157482	12.884922	17.916473	12.6352
	13.291116	13.242955	13.227623	12.85396	13.807293
	17.916473	12.467784	13.409009	11.759263	14.769379
	15.704796	12.404451	14.156532	13.672841	12.624996
	15.312495	15.271314	17.916473	15.022164	15.022164
	17.001385	16.146549	15.327678	14.865213	15.41269
	14.82543	15.395535	14.720925	14.527216	15.704796
	17.916473	14.462834	14.720925	14.064812	14.896075
	15.124483	14.714641			
Yamaceratopsdorngobiensis	16.321389	9.748846	13.113617	14.92222	
	14.527216	15.038711	16.152709	14.388885	13.990738
	15.384859	11.97219	15.123133	11.677738	0 10.350185
	9.307363	11.133733	11.164186	10.922818	14.615014
	10.321367	10.592778	10.447033	8.9861	10.541073 11.369186

11.446325 10.911921 10.709646 13.948341 17.916473

10.759793 12.853174 12 13.213168 17.916473 10.860939

13.789476 12.404451 10.860939 16.152709 15.215805

17.916473 15.041609 14.911776 17.916473 16.664609

13.948341 13.589541 10.805554 15.41269 16.086246

14.838228 14.838228 17.916473 17.916473 14.04622

14.640617 15.215805 13.037838 14.255776 9.013878

Archaeoceratopsoshimai 16.649538 8.566833 13.603768 14.992687

13.502783 14.185698 13.785774 14.472042 13.576174

13.078467 17.916473 14.14639 12.083693 10.350185 0

7.925627 11.043513 10.271509 10.951844 16.948998

8.581375 11.905295 11.735164 17.916473 11.076404

12.599072 12.213108 10.722589 11.172438 13.126228

17.916473 9.526279 14.243688 13.983387 13.831973

15.704796 13.785774 13.598715 12.734309 13.658788

14.255776 14.191251 17.916473 14.66009 14.734684

15.583324 14.911776 14.026877 14.626008 13.865371

14.723626 14.462834 14.626761 15.011587 15.953637

15.953637 14.527216 14.720925 13.948341 13.882109

13.477795 13.520817

Archaeoceratopsyujingziensis13.983387 7.658057 12.027746 13.732126

10.593601 13.413082 14.714641 13.520817 10.321367

12.853174 17.916473 13.741065 11.901018 9.307363

7.925627 0 9.190901 10.593601 10.04782 15.864369

3.693237 9.027658 9.919001 17.916473 11.180625

10.576463	10.083262	9.637755	8.885651	13.196543
15.384859	10.970871	12.624975	9.041571	12.356402
17.916473	13.520817	13.249906	11.142594	12.055428
11.281207	12.624975	17.916473	12.785697	13.078467
14.361058	14.986105	14.255776	12.964467	14.160703
14.160703	12.45633	14.416657	14.986105	14.361058
15.953637	14.160703	13.249906	15.953637	12.524606
12.45633	11.281207			
Auroraceratopsrugosus	16.266127	9.205976	14.101484	13.986362
13.03652	14.01249	15.011587	14.615253	13.603768
14.160436	17.916473	12.451129	13.613786	11.133733
11.043513	9.190901	0	11.364006	12.624996 15.704796
7.789318	9.942747	10.869052	17.916473	10.832472
12.547697	13.213168	12.727922	10.812606	14.615253
15.953637	10.726719	15.638841	15.013882	13.113978
17.916473	15.468203	15.395535	13.182394	15.788148
14.855984	14.975167	17.916473	15.551101	15.551101
15.041609	14.966312	14.935398	14.031735	15.981471
15.395535	15.260226	15.461087	15.395535	16.566166
17.916473	15.583044	15.395535	15.715903	13.088013
14.66009	13.865371			
Helioceratopsbrachygnathus	14.958275	8.9861	17.916473	15.013882
11.97219	14.986105	17.916473	17.916473	17.916473
17.916473	17.916473	14.838228	13.865371	11.164186
10.271509	10.593601	11.364006	0	12.624975 14.958275

	17.916473	11.364006	11.656434	17.916473	14.714641
	11.50936	10.970871	9.677629	9.17878	14.986105
	17.916473	14.361058	17.916473	17.916473	11.50936
	17.916473	17.916473	10.805554	17.916473	17.916473
	9.013878	0	17.916473	10.805554	10.805554
	17.916473	10.805554	10.805554	10.916043	9.013878
	9.013878	10.805554	13.465233	17.916473	8.9861
	8.9861	11.97219	13.465233	17.916473	10.916043
	10.805554	17.916473			
Graciliceratopsmongoliensis	16.080355	10.860939	14.388885	15.049718	
	16.594003	15.639865	16.749925	15.583324	14.986105
	16.152709	13.465233	13.514281	12.600423	10.922818
	10.951844	10.04782	12.624996	12.624975	0
	14.160703	17.916473	10.306618	11.618915	6.027714
	9.676987	12.17535	10.7473	9.5	9.952688
	11.905821	17.916473	10.208391	12.45633	12.055428
	12.844319	13.465233	13.249906	13.81201	13.576174
	13.249906	13.520817	14.714641	17.916473	12.963843
	12.963843	14.958275	14.838228	13.576174	13.521051
	10.064606	10.916043	13.196543	14.255776	12.908627
	9.013878	17.916473	13.548524	11.656434	14.986105
	13.529552	13.548524			
	11.281207				
Zhuchengceratopsinexpectus	15.161055	17.916473	17.916473	14.855984	
	17.916473	16.948998	17.916473	17.916473	17.916473
	17.916473	17.916473	17.091192	15.271314	14.615014
	16.948998	15.864369	15.704796	14.958275	14.160703
	0				

	17.916473	9.233093	10.916043	17.916473	11.142594
	8.726938	10.567567	10.04782	10.726719	10.589893
	17.916473	12.110601	9.013878	9.013878	12.014211
	17.916473	9.013878	12 12	9.013878	10.805554 0
	17.916473	10.321367	10.321367	8.9861 10.321367	11.281207
	12.014211	11.97219	9.041571	10.321367	9.041571
	9.013878	9.013878	13.465233	10.805554	9.041571
	13.465233	12.014211	10.321367	8.9861	
Ajkaceratopskozmai	17.916473	9.013878	17.916473	15.732629	
	13.113617	13.113617	17.916473	17.916473	17.916473
	17.916473	17.916473	10.589893	6.137318	10.321367
	8.581375	3.693237	7.789318	17.916473	17.916473
	17.916473	0 0	6.082763	17.916473	5.256677
	8.085722	5.075431	4.172219	6.645161	11.97219
	17.916473	8.9861 7.249828	9.013878	9.705882	0
	10.064606	10.064606	7.249828	10.860939	17.916473
	4.562072	17.916473	11.51248	11.51248	17.916473
	17.916473	10.860939	10.404081	17.916473	10.805554
	10.805554	10.805554	12.853174	17.916473	17.916473 12
	12 9.013878	10.404081	12	17.916473	
Montanoceratopscerorhynchus		16.649538	7.898592	13.865371	
	16.108593	14.366107	15.140947	14.838228	14.640617
	13.520817	13.990738	12.027746	14.993579	12.157482
	10.592778	11.905295	9.027658	9.942747	11.364006
	10.306618	9.233093	0 0	8.123072	8.085722

	8.256954	10.021942	10.450582	9.300629	9.960515
	11.862023	17.916473	9.942747	13.81201	12.908627
	12.762305	17.916473	13.249906	13.789476	11.063731
	13.249906	13.113617	14.416657	17.916473	14.472042
	14.609867	17.916473	15.013882	13.465395	12.950813
	7.249828	13.078467	14.609867	14.160436	13.078467
	10.805554	17.916473	13.340418	12.785697	14.640617
	12.719605	12.707872	11.281207		
Prenoceratopspieganensis	16.720237	7.898592	16.315586	15.205482	
	14.134201	14.382641	15.732629	16.451317	15.953637
	15.953637	11.97219	15.003806	12.884922	10.447033
	11.735164	9.919001	10.869052	11.656434	11.618915
	10.916043	6.082763	8.123072	0	8.9861 9.01675
	9.451243	12.138777	11.480937	11.328554	11.7315
	17.916473	10.344201	15.41269	14.714641	12.819594
	17.916473	14.838228	16.180544	13.514281	14.838228
	16.315586	15.981471	17.916473	15.932689	15.849997
	17.916473	16.824577	14.966312	12.596296	17.916473
	15.981471	16.414238	16.265861	15.864369	14.361058
	17.916473	15.171047	15.556814	15.864369	12.748395
	16.265861	15.704796			
Bainoceratopsefremovi	17.916473	17.916473	17.916473	15.171047	
	17.916473	15.953637	17.916473	17.916473	17.916473
	17.916473	7.249828	17.916473	17.916473	8.9861 17.916473
	17.916473	17.916473	17.916473	6.027714	17.916473

	17.916473	8.085722	8.9861 0	8.309608	11.142594
	9.233093	17.916473	11.97219	17.916473	17.916473
	9.013878	17.916473	17.916473	13.576174	17.916473
	17.916473	17.916473	14.361058	17.916473	17.916473
	17.916473	17.916473	17.916473	17.916473	17.916473
	17.916473	17.916473	13.576174	17.916473	17.916473
	17.916473	17.916473	17.916473	17.916473	17.916473
	17.916473	17.916473	17.916473	13.576174	17.916473
	17.916473				
Udanoceratopstschizhovi		17.076373	7.658057	15.953637	15.404949
	14.243688	14.762697	16.566166	16.315586	15.953637
	17.916473	10.805554	14.211367	12.6352	10.541073
	11.076404	11.180625	10.832472	14.714641	9.676987
	11.142594	5.256677	8.256954	9.01675	8.309608 0
	9.010282	11.13969	11.434937	10.444733	12.060759
	17.916473	9.447222	13.249906	11.51248	12.239364
	17.916473	12.707872	12.963843	12.624996	12.110601
	17.916473	11.656434	17.916473	12.657477	12.657477
	17.916473	17.916473	12.604852	12.320629	13.493054
	13.81201	14.255776	14.04622	13.548524	17.916473
	17.916473	13.078467	13.340418	15.41269	12.150579
	14.04622	14.388885			
Leptoceratopsgracilis		16.246075	10.509202	15.556464	15.75988
	14.728411	15.052467	15.051646	16.37121	15.932689
	16.479153	13.493054	15.575856	13.291116	11.369186

12.599072 10.576463 12.547697 11.50936 12.17535

8.726938 8.085722 10.021942 9.451243 11.142594

9.010282 0 13.574772 12.830256 12.02183 14.434128

16.566166 11.127107 15.998893 15.395535 14.953929

17.280785 15.558268 16.224303 14.248425 15.73876

17.133064 16.392642 17.916473 15.927379 16.090078

16.633482 17.389204 15.794186 15.157647 16.585525

16.268661 16.502953 16.904779 16.717179 17.197838

17.496446 16.597028 16.015692 16.772119 15.031614

16.353932 15.849997

Protoceratopsandrewsi 17.344512 9.367497 16.266127 16.386446

15.716437 16.090078 16.19013 16.918285 16.645048

17.227699 12.027746 15.27406 13.242955 11.446325

12.213108 10.083262 13.213168 10.970871 10.7473

10.567567 5.075431 10.450582 12.138777 9.233093

11.13969 13.574772 0 10.916191 9.610427 15.342332

16.824577 11.249725 15.520675 15.639865 14.803057

14.444376 15.693769 15.66198 13.998313 15.817045

16.502202 15.363558 17.916473 15.887257 16.026172

15.984947 17.25714 15.279515 15.032218 15.051646

16.199249 16.476512 16.5791 16.413018 17.227699

16.585525 16.229831 15.592682 16.390262 14.857328

16.060208 15.041609

Protoceratopshellenikorhinus 17.420922 8.955356 16.080355 16.043768

15.804657 15.936039 16.464284 16.816293 16.479153

17.129972 17.916473 14.375438 13.227623 10.911921

10.722589 9.637755 12.727922 9.677629 9.5 10.04782

4.172219 9.300629 11.480937 17.916473 11.434937

12.830256 10.916191 0 8.953234 14.540648 16.451317

9.751961 15.179482 15.255922 14.006543 14.838228

15.578635 15.455555 14.037895 15.708792 15.788451

15.381079 17.916473 15.500514 15.689492 15.698776

16.649757 14.841688 14.339931 14.264152 15.73876

15.885219 16.224303 16.199249 16.265861 16.266127

16.157173 15.478413 16.368779 14.088323 15.771932

14.255776

Bagaceratopsrozhdestvenskyi 17.133064 10.335647 15.373404 15.288317

14.745847 15.306866 16.320311 16.080355 15.66304

16.265861 6.027714 14.817207 12.85396 10.709646

11.172438 8.885651 10.812606 9.17878 9.952688

10.726719 6.645161 9.960515 11.328554 11.97219

10.444733 12.02183 9.610427 8.953234 0 12.14453

17.916473 10.300435 11.963146 10.593601 12.165355

15.704796 11.793504 13.598715 12.062973 12.790231

14.444376 12.763261 17.916473 12.848396 13.318707

15.732629 15.271314 11.958328 12.322297 11.164186

12.763261 13.292879 13.921998 13.807293 13.493054

15.953637 13.477795 12.745279 13.514281 12.001949

13.713588 10.589893

Zuniceratopschristopheri 15.468203 13.990738 17.916473 15.064617
15.788148 14.366107 17.916473 17.916473 15.953637
17.916473 17.916473 15.760413 13.807293 13.948341
13.126228 13.196543 14.615253 14.986105 11.905821
10.589893 11.97219 11.862023 11.7315 17.916473
12.060759 14.434128 15.342332 14.540648 12.14453 0
11.50936 13.093754 13.166511 11.759263 11.386212
12.45633 13.033491 11.396945 13.033491 13.292879
10.647953 10.315679 12.027746 9.60721 9.785193
9.231144 10.602236 10.451689 10.146052 11.180625
10.124558 9.01675 11.435532 10.629468 8.085722
11.650036 11.251775 9.077479 10.496913 10.72191
10.306618 10.970871

Turanoceratopstardabilis 14.361058 0 17.916473 17.916473
16.152709 17.916473 17.916473 17.916473 17.916473
17.916473 17.916473 17.916473 17.916473 17.916473
17.916473 15.384859 15.953637 17.916473 17.916473
17.916473 17.916473 17.916473 17.916473 17.916473
17.916473 16.566166 16.824577 16.451317 17.916473
11.50936 0 17.916473 9.813347 4.562072 10.04782
7.249828 9.813347 10.271509 12.514843 9.813347
11.312205 10.916043 11.281207 10.04782 10.04782
9.748846 10.04782 11.50936 11.312205 12.514843
11.142594 8.237224 10.835262 9.705882 7.249828

11.50936 11.622506 9.124144 10.970871 11.622506

12.785697 12.027746

Cerasinopshodgskissi 16.90306 10.064606 13.113617 14.664242

13.948341 14.894766 15.215805 14.986105 13.990738

14.958275 17.916473 13.929944 12.467784 10.759793

9.526279 10.970871 10.726719 14.361058 10.208391

12.110601 8.9861 9.942747 10.344201 9.013878 9.447222

11.127107 11.249725 9.751961 10.300435 13.093754

17.916473 0 11.656434 9.911176 13.389379 13.465233

12.45633 14.255776 9.649823 12.083046 13.990738

12.908627 17.916473 14.322731 14.322731 14.958275

15.583324 13.409009 13.707523 12.624975 12.45633

13.983387 13.983387 12.785697 13.465233 17.916473

13.340418 13.078467 13.249906 13.306108 13.078467

12.624975

Achelousaurushorneri 15.312495 15.215805 16.890447 16.510896

15.212955 16.208331 17.916473 17.129972 17.001385

17.916473 17.916473 14.714641 13.409009 12.853174

14.243688 12.624975 15.638841 17.916473 12.45633

9.013878 7.249828 13.81201 15.41269 17.916473

13.249906 15.998893 15.520675 15.179482 11.963146

13.166511 9.813347 11.656434 0 6.002839 6.619692

5.814697 5.519999 5.595757 5.651087 6.139436

6.855655 7 10.007029 10.111874 10.258284 12.89328

10.812606 9.733961 10.746273 11.862023 9.826096

	9.255278	10.008142	10.812606	11.656434	10.832472
	10.399064	9.297225	10.083262	10.088646	9.512915
	6.092919				
Avaceratopslammersi	13.520817	15.384859	16.451317	15.788148	
	16.208331	16.180544	17.916473	16.664609	16.566166
	17.916473	17.916473	13.990738	11.759263	12 13.983387
	9.041571	15.013882	17.916473	12.055428	9.013878
	9.013878	12.908627	14.714641	17.916473	11.51248
	15.395535	15.639865	15.255922	10.593601	11.759263
	4.562072	9.911176	6.002839	0 5.827729	10.404081
	5.800916	6.533041	7.08268	6.002839	5.12638
	6.893043	4.562072	7.254523	7.269593	11.839447
	7.079783	8.134602	7.254523	9.705882	8.417881
	6.484087	6.484087	8.134602	8.101212	8.581375
	7.531001	7.915864	7.242674	7.386411	8.581328
	5.075431				
Centrosaurusapertus	16.333341	12.220202	15.566985	16.375853	
	14.552194	15.598 15.69416	15.326621	14.615253	15.468203
	15.953637	15.910905	14.769379	13.213168	13.831973
	12.356402	13.113978	11.50936	12.844319	12.014211
	9.705882	12.762305	12.819594	13.576174	12.239364
	14.953929	14.803057	14.006543	12.165355	11.386212
	10.04782	13.389379	6.619692	5.827729	0 5.497378
	6.551953	5.842537	8.473551	5.917915	7.082598
	7.264115	7.987694	9.388259	9.652171	10.227285

9.477338	8.805319	10.395125	10.124558	9.4724	9.157103
9.72058	10.266479	10.241321	8.700619	10.100801	
9.039774	9.431486	10.104643	9.001086	5.644497	
Rubeosaurusovatus	17.916473	14.958275	17.916473	17.916473	
15.171047	17.916473	17.916473	17.916473	17.916473	
17.916473	17.916473	17.916473	15.704796	17.916473	
15.704796	17.916473	17.916473	17.916473	13.465233	
17.916473	0	17.916473	17.916473	17.916473	17.916473
17.280785	14.444376	14.838228	15.704796	12.45633	
7.249828	13.465233	5.814697	10.404081	5.497378	0
6.10497	4.691141	4.521528	3.883594	6.894722	
6.18954	8.101212	11.025425	10.567567	10.970871	
10.593601	9.26013	11.180625	10.404081	9.26013	
8.897335	9.645642	10.335647	11.97219	11.656434	
9.287088	9.677629	9.287088	10.919835	10.102104	
7.658057					
Pachyrhinosauruscanadensis	15.041609	13.865371	16.749925	16.510896	
15.003806	16.266127	17.916473	17.048534	16.890447	
17.916473	17.916473	15.732629	12.404451	10.860939	
13.785774	13.520817	15.468203	17.916473	13.249906	
9.013878	10.064606	13.249906	14.838228	17.916473	
12.707872	15.558268	15.693769	15.578635	11.793504	
13.033491	9.813347	12.45633	5.519999	5.800916	
6.551953	6.10497	0	5.766169	6.362619	6.440178
7.158456	7.198215	8.144489	9.918765	10.303426	

12.922982 10.809804 9.368232 10.928681 12.247449

9.976099 9.605362 10.136567 11.13969 12.45633

10.509202 10.518366 9.336831 10.213417 9.949267

9.153818 6.092919

Pachyrhinosauruslakustai 14.499655 12.908627 15.981471 16.26104

14.81245 15.972089 17.16538 16.180544 15.981471

16.824577 17.916473 15.312495 14.156532 13.789476

13.598715 13.249906 15.395535 10.805554 13.81201 12

10.064606 13.789476 16.180544 17.916473 12.963843

16.224303 15.66198 15.455555 13.598715 11.396945

10.271509 14.255776 5.595757 6.533041 5.842537

4.691141 5.766169 0 5.72822 6.19105 5.713227

6.311682 5.897894 8.731621 8.739815 10.580761

8.701887 8.495299 9.001086 9.473648 9.451243

8.898356 8.254896 8.862381 11.715016 7.915864

8.090013 8.408805 8.030295 8.457479 8.665404

5.752391

Einiosaurusprocurvicornis 14.966312 13.548524 14.737483 15.166761

14.031735 15.103921 15.856015 15.373404 14.472042

15.440472 11.97219 15.556814 13.672841 12.404451

12.734309 11.142594 13.182394 17.916473 13.576174 12

7.249828 11.063731 13.514281 14.361058 12.624996

14.248425 13.998313 14.037895 12.062973 13.033491

12.514843 9.649823 5.651087 7.08268 8.473551

4.521528 6.362619 5.72822 0 5.766169 7.310414

7.621108 7.651356 9.682019 9.750636 11.570213

10.854032 9.574915 10.877978 10.162797 10.013639

9.962429 9.76097 9.718913 10.404081 8.552586

9.410176 8.990225 7.522743 10.660625 8.489982

4.691141

Styracosaurusalbertensis 15.312495 14.160703 15.013882 16.119921

14.63694 15.340758 16.479153 15.556814 15.171047

15.732629 17.916473 15.583324 12.624996 10.860939

13.658788 12.055428 15.788148 17.916473 13.249906

9.013878 10.860939 13.249906 14.838228 17.916473

12.110601 15.73876 15.817045 15.708792 12.790231

13.292879 9.813347 12.083046 6.139436 6.002839

5.917915 3.883594 6.440178 6.19105 5.766169 0

7.310414 7.275457 8.566833 10.394649 10.77066

12.436104 11.019476 9.697727 11.193998 11.923197

9.826096 9.569619 10.687651 11.536079 11.364006

10.759793 11.100824 9.412883 10.462373 10.673317

9.067931 5.497378

Albertaceratopsnesmoi 14.615014 14.388885 15.953637 16.464284

16.419116 16.538875 16.749925 16.566166 16.152709

16.152709 17.916473 15.953637 15.312495 16.152709

14.255776 11.281207 14.855984 9.013878 13.520817

10.805554 17.916473 13.113617 16.315586 17.916473

17.916473 17.133064 16.502202 15.788451 14.444376

10.647953 11.312205 13.990738 6.855655 5.12638

	7.082598	6.894722	7.158456	5.713227	7.310414
	7.310414	0	6.214107	6.623632	9.81199	10.087121
	10.443759	9.592123	8.419988	9.716583	9.68967
	9.093182	9.50025	9.953638	10.174286	9.287088
	7.244149	9.728199	8.82123	9.142246	9.37481
	8.458566	6.623632			
Diabioceratopseatoni	14.322731	14.838228	16.824577	16.778408	
	15.003806	16.419116	17.197838	17.048534	15.864369
	16.749925	17.916473	16.451317	15.271314	15.215805
	14.191251	12.624975	14.975167	0	14.714641	0
	4.562072	14.416657	15.981471	17.916473	11.656434
	16.392642	15.363558	15.381079	12.763261	10.315679
	10.916043	12.908627	7	6.893043	7.264115	6.18954
	7.198215	6.311682	7.621108	7.275457	6.214107	0
	6.623632	10.213261	10.626476	10.585701	10.213417
	8.821356	10.088646	11.133733	9.370043	10.03743
	10.332772	10.651947	11.759263	9.231144	10.31238
	9.72721	9.718913	9.882315	9.189879	8.897335
Sinoceratopszhuchengensis	17.916473	17.916473	17.916473	17.916473	
	15.704796	17.916473	17.916473	17.916473	17.916473
	17.916473	17.916473	17.916473	17.916473	17.916473
	17.916473	17.916473	17.916473	17.916473	17.916473
	17.916473	17.916473	17.916473	17.916473	17.916473
	17.916473	17.916473	17.916473	17.916473	17.916473
	12.027746	11.281207	17.916473	10.007029	4.562072

	7.987694	8.101212	8.144489	5.897894	7.651356
	8.566833	6.623632	6.623632	0	10.638979 10.638979
	10.271509	10.335647	8.085722	9.9766	7.658057 9.17878
	10.726719	10.007029	10.335647	7.789318	4.723611
	9.645642	8.462238	9.287088	9.645642	7.658057
	2.202692				
Chasmosaurusrusselli	14.134201	15.981471	16.265861	16.133768	
	15.862103	15.651481	17.366407	16.594003	15.556814
	16.948998	17.916473	15.66304	15.022164	15.041609
	14.66009	12.785697	15.551101	10.805554	12.963843
	10.321367	11.51248	14.472042	15.932689	17.916473
	12.657477	15.927379	15.887257	15.500514	12.848396
	9.60721	10.04782	14.322731	10.111874	7.254523
	9.388259	11.025425	9.918765	8.731621	9.682019
	10.394649	9.81199	10.213261	10.638979	0 6.757421
	7.29323	7.409087	7.210409	7.759267	7.509369
	8.342168	7.179821	8.836725	9.434188	9.058273
	6.904105	9.133737	8.16499	8.691501	8.776723
	8.010216	3.541783			
Chasmosaurusbelli	14.134201	16.180544	16.343422	16.333341	
	15.926099	15.651481	17.401434	16.645048	15.66304
	17.001385	17.916473	15.66304	15.022164	14.911776
	14.734684	13.078467	15.551101	10.805554	12.963843
	10.321367	11.51248	14.609867	15.849997	17.916473
	12.657477	16.090078	16.026172	15.689492	13.318707

9.785193 10.04782 14.322731 10.258284 7.269593

9.652171 10.567567 10.303426 8.739815 9.750636

10.77066 10.087121 10.626476 10.638979 6.757421 0

7.234178 7.437312 7.328229 8.158598 7.959899

7.965167 7.055068 9.106863 9.692926 9.058273

7.334918 9.39946 8.183362 8.806858 9.138491

7.800111 3.541783

Mojoceratopsperifania 14.640617 17.916473 15.704796 16.146549

17.003738 17.001385 16.664609 15.953637 15.704796

15.704796 17.916473 17.916473 17.001385 17.916473

15.583324 14.361058 15.041609 17.916473 14.958275

8.9861 17.916473 17.916473 17.916473 17.916473 17.916473

16.633482 15.984947 15.698776 15.732629 9.231144

9.748846 14.958275 12.89328 11.839447 10.227285

10.970871 12.922982 10.580761 11.570213 12.436104

10.443759 10.585701 10.271509 7.29323 7.234178 0

7.164244 7.96009 8.328265 8.552586 9.626962

7.847768 9.687089 9.88686 8.76138 7.966399

9.483709 9.210863 9.836158 9.687089 9.483709

4.134844

Agujaceratopsmariscalensis 14.737483 15.953637 14.388885 15.984947

16.019439 15.556464 15.013882 14.416657 14.714641

14.714641 17.916473 16.566166 16.146549 16.664609

14.911776 14.986105 14.966312 10.805554 14.838228

10.321367 17.916473 15.013882 16.824577 17.916473

	17.916473	17.389204	17.25714	16.649757	15.271314
	10.602236	10.04782	15.583324	10.812606	7.079783
	9.477338	10.593601	10.809804	8.701887	10.854032
	11.019476	9.592123	10.213417	10.335647	7.409087
	7.437312	7.164244	0	6.222632	7.325481
	7.38347				
	8.701887	7.391023	8.529986	9.158688	7.125
	8.171814				
	9.388376	9.048133	9.417138	9.250884	8.478445
	3.402587				
Utahceratopsgettyi	14.421815	15.864369	15.66304	15.704667	
	15.17627	14.935398	16.320311	15.271314	15.66304
	16.265861	17.916473	15.373404	15.327678	13.948341
	14.026877	14.255776	14.935398	10.805554	13.576174
	11.281207	10.860939	13.465395	14.966312	17.916473
	12.604852	15.794186	15.279515	14.841688	11.958328
	10.451689	11.50936	13.409009	9.733961	8.134602
	8.805319	9.26013	9.368232	8.495299	9.574915
	9.697727	8.419988	8.821356	8.085722	7.210409
	7.328229	7.96009	6.222632	0	6.301771
	6.708204				
	7.379832	7.209206	7.264115	8.308048	9.058273
	5.489786	7.680762	7.954778	7.27405	8.162261
	8.129727	2.062355			
Pentaceratopssternbergii	16.199249	13.785774	16.266127	16.28506	
	15.529992	15.589367	16.19013	16.320311	15.373404
	15.932689	15.704796	16.344244	14.865213	13.589541
	14.626008	12.964467	14.031735	10.916043	13.521051

12.014211 10.404081 12.950813 12.596296 13.576174

12.320629 15.157647 15.032218 14.339931 12.322297

10.146052 11.312205 13.707523 10.746273 7.254523

10.395125 11.180625 10.928681 9.001086 10.877978

11.193998 9.716583 10.088646 9.9766 7.759267 8.158598

8.328265 7.325481 6.301771 0 7.133853 7.462468

7.569321 8.689902 9.701496 9.058273 6.736381

9.388964 8.471127 8.252528 9.712535 8.176421

3.883594

Coahuilaceratopsmagnacuerna 17.916473 15.953637 14.361058

16.180544 16.343422 15.41269 17.916473 15.384859

14.361058 17.916473 17.916473 12.027746 15.41269

10.805554 13.865371 14.160703 15.981471 9.013878

10.064606 11.97219 17.916473 7.249828 17.916473

17.916473 13.493054 16.585525 15.051646 14.264152

11.164186 11.180625 12.514843 12.624975 11.862023

9.705882 10.124558 10.404081 12.247449 9.473648

10.162797 11.923197 9.68967 11.133733 7.658057

7.509369 7.959899 8.552586 7.38347 6.708204

7.133853 0 7.244149 7.386411 7.158456 7.918913

5.075431 6.406298 7.884161 8.321352 7.687409

8.081736 6.791258 4.354648

Kosmoceratopsrichardsoni 12.829204 16.566166 16.824577 15.551101

16.054763 16.506943 17.916473 16.948998 16.824577

17.916473 17.916473 14.640617 14.82543 15.41269

14.723626 14.160703 15.395535 9.013878 10.916043

9.041571 10.805554 13.078467 15.981471 17.916473

13.81201 16.268661 16.199249 15.73876 12.763261

10.124558 11.142594 12.45633 9.826096 8.417881

9.4724 9.26013 9.976099 9.451243 10.013639 9.826096

9.093182 9.370043 9.17878 8.342168 7.965167

9.626962 8.701887 7.379832 7.462468 7.244149 0

7.50735 7.981106 8.350952 7.987694 6.708204

8.721616 8.60277 8.4 8.779989 8.659896 3.1261

Vagaceratopsirvinensis 13.558219 16.749925 16.086246 16.071543

16.020378 16.361073 17.326548 16.414238 16.180544

16.948998 17.916473 15.013882 15.395535 16.086246

14.462834 12.45633 15.260226 10.805554 13.196543

10.321367 10.805554 14.609867 16.414238 17.916473

14.255776 16.502953 16.476512 15.885219 13.292879

9.01675 8.237224 13.983387 9.255278 6.484087

9.157103 8.897335 9.605362 8.898356 9.962429

9.569619 9.50025 10.03743 10.726719 7.179821

7.055068 7.847768 7.391023 7.209206 7.569321

7.386411 7.50735 0 8.263485 8.521391 7.987694

7.158456 9.109522 8.12076 8.665845 8.693846

7.844409 3.23306

Anchiceratopsornatus 14.527216 15.864369 15.981471 16.368779

15.863052 16.689023 17.304484 16.414238 16.086246

16.890447 17.916473 15.732629 14.720925 14.838228

	14.626761	14.416657	15.461087	13.465233	14.255776
	9.041571	10.805554	14.160436	16.265861	17.916473
	14.04622	16.904779	16.5791	16.224303	13.921998
	11.435532	10.835262	13.983387	10.008142	6.484087
	9.72058	9.645642	10.136567	8.254896	9.76097
	10.687651	9.953638	10.332772	10.007029	8.836725
	9.106863	9.687089	8.529986	7.264115	8.689902
	7.158456	7.981106	8.263485	0	7.81025 5.882434
	7.036009	8.550471	7.816204	7.760432	8.259964
	7.015107	4.2			
Arrhinoceratopsbrachyops	14.499655	15.732629	15.864369	15.910356	
	15.286142	16.036994	17.16538	16.086246	15.013882
	16.749925	17.916473	15.583324	14.527216	14.838228
	15.011587	14.986105	15.395535	17.916473	12.908627
	9.013878	12.853174	13.078467	15.864369	17.916473
	13.548524	16.717179	16.413018	16.199249	13.807293
	10.629468	9.705882	12.785697	10.812606	8.134602
	10.266479	10.335647	11.13969	8.862381	9.718913
	11.536079	10.174286	10.651947	10.335647	9.434188
	9.692926	9.88686	9.158688	8.308048	9.701496
	7.918913	8.350952	8.521391	7.81025	0 6.403124
	7.019282	8.345722	7.789025	7.843525	8.572902
	7.038285	4.103657			
Ojoceratopsfowleri	13.990738	17.916473	17.916473	15.215805	
	17.916473	15.953637	17.916473	17.916473	17.916473

	17.916473	17.916473	14.958275	15.704796	17.916473
	15.953637	14.361058	16.566166	8.9861	9.013878 9.013878
	17.916473	10.805554	14.361058	17.916473	17.916473
	17.197838	17.227699	16.265861	13.493054	8.085722
	7.249828	13.465233	11.656434	8.101212	10.241321
	11.97219	12.45633	11.715016	10.404081	11.364006
	9.287088	11.759263	7.789318	9.058273	9.058273
	8.76138	7.125	9.058273	9.058273	5.075431 7.987694
	7.987694	5.882434	6.403124	0	4.134844 6.10497
	5.496035	4.879805	6.882765	5.882434	0
Eotriceratopsxerinsularis	16.152709	17.916473	17.916473	17.916473	
	17.304484	17.916473	17.916473	17.916473	17.916473
	17.916473	17.916473	17.916473	17.916473	17.916473
	15.953637	15.953637	17.916473	8.9861	17.916473 13.465233
	17.916473	17.916473	17.916473	17.916473	17.916473
	17.496446	16.585525	16.266127	15.953637	11.650036
	11.50936	17.916473	10.832472	8.581375	8.700619
	11.656434	10.509202	7.915864	8.552586	10.759793
	7.244149	9.231144	4.723611	6.904105	7.334918
	7.966399	8.171814	5.489786	6.736381	6.406298
	6.708204	7.158456	7.036009	7.019282	4.134844 0
	5.526595	5.440435	5.130833	5.170322	4.74257
	2.395984				
Torosauruslatus	14.723626	15.864369	15.440472	15.998893	
	15.041592	15.639865	16.777763	15.849997	15.556814

	16.086246	17.916473	15.732629	14.462834	14.04622
	14.527216	14.160703	15.583044	11.97219	13.548524
	10.805554	12	13.340418	15.171047	17.916473	13.078467
	16.597028	16.229831	16.157173	13.477795	11.251775
	11.622506	13.340418	10.399064	7.531001	10.100801
	9.287088	10.518366	8.090013	9.410176	11.100824
	9.728199	10.31238	9.645642	9.133737	9.39946
	9.483709	9.388376	7.680762	9.388964	7.884161
	8.721616	9.109522	8.550471	8.345722	6.10497
	5.526595	0	6.113803	6.671048	7.335871	5.631669
	4.301094				
Torosaurusutahensis	14.101484	16.824577	15.013882	15.38173	
	14.430165	14.462834	16.538875	15.312495	14.04622
	15.41269	17.916473	14.838228	14.720925	14.640617
	14.720925	13.249906	15.395535	13.465233	11.656434
	9.041571	12	12.785697	15.556814	17.916473	13.340418
	16.015692	15.592682	15.478413	12.745279	9.077479
	9.124144	13.078467	9.297225	7.915864	9.039774
	9.677629	9.336831	8.408805	8.990225	9.412883
	8.82123	9.72721	8.462238	8.16499	8.183362
	9.210863	9.048133	7.954778	8.471127	8.321352
	8.60277	8.12076	7.816204	7.789025	5.496035
	5.440435	6.113803	0	6.443848	6.204354	5.744395
	2.925734				

Nedoceratopshatcheri	14.966312	16.664609	15.215805	15.744285
15.483829	16.320311	17.129972	16.824577	16.566166
16.566166	17.916473	17.916473	14.064812	15.215805
13.948341	15.953637	15.715903	17.916473	14.986105
13.465233	9.013878	14.640617	15.864369	17.916473
15.41269	16.772119	16.390262	16.368779	13.514281
10.496913	10.970871	13.249906	10.083262	7.242674
9.431486	9.287088	10.213417	8.030295	7.522743
10.462373	9.142246	9.718913	9.287088	8.691501
8.806858	9.836158	9.417138	7.27405	8.252528
7.687409	8.4	8.665845	7.760432	7.843525	4.879805
5.130833	6.671048	6.443848	0	6.399169	4.925401
4.229731				
Triceratopshorridus	16.312277	13.422693	15.096909	16.138566
14.633711	15.075479	15.69416	15.254081	14.723626
15.556464	15.704796	15.953546	14.896075	13.037838
13.882109	12.524606	13.088013	10.916043	13.529552
12.014211	10.404081	12.719605	12.748395	13.576174
12.150579	15.031614	14.857328	14.088323	12.001949
10.72191	11.622506	13.306108	10.088646	7.386411
10.104643	10.919835	9.949267	8.457479	10.660625
10.673317	9.37481	9.882315	9.645642	8.776723
9.138491	9.687089	9.250884	8.162261	9.712535
8.081736	8.779989	8.693846	8.259964	8.572902

6.882765 5.170322 7.335871 6.204354 6.399169 0
5.819811 3.541783

Triceratopsprorsus 14.243688 15.583324 13.782946 14.822323
14.121261 14.120863 15.788148 14.737483 13.782946
14.615014 17.916473 14.838228 15.124483 14.255776
13.477795 12.45633 14.66009 10.805554 13.548524
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16.353932 16.060208 15.771932 13.713588 10.306618
12.785697 13.078467 9.512915 8.581328 9.001086
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8.659896 7.844409 7.015107 7.038285 5.882434
4.74257 5.631669 5.744395 4.925401 5.819811 0
2.840765

Tatankaceratopssacrisonorum 15.215805 15.704796 14.388885 14.444376
14.160436 14.640617 16.566166 15.215805 13.113617
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11.281207 13.865371 17.916473 11.281207 8.9861 17.916473
11.281207 15.704796 17.916473 14.388885 15.849997
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6.092919 5.752391 4.691141 5.497378 6.623632
8.897335 2.202692 3.541783 3.541783 4.134844
3.402587 2.062355 3.883594 4.354648 3.1261 3.23306

4.2	4.103657	0	2.395984	4.301094	2.925734
4.229731	3.541783	2.840765	0		

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